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The cottontail rabbit is one of the most important game animals in the United States, yet little effort heretofore has been made to determine the habitat requirements and to develop management measures for this species. The two most extensive studies of this nature to date have been those of Trippensee (1934) and Allen (1938a). When we consider that the annual kill of cottontails in Michigan alone is over 2,000,000 individuals, it becomes apparent that this species is worthy of detailed investigation to formulate a basis for sound management. The huge numbers of cottontails imported by various eastern states for planting prove that those states were in need of better methods for properly managing their native cottontail populations.

The present study was initiated in January, 1938, and terminated in December of 1939. Information here presented represents part of the data collected while studying the effects of various proposed management measures on populations of the cottontail (*Sylvilagus floridanus mearnsii*).

Grateful acknowledgement is made to the Michigan Department of Conservation for providing the part-time fellowship and other support which made this study possible. The encouragement and advice of H. D. Ruhl, chief of the Game Division is appreciated. Dr. Lee R. Dice of the University of Michigan directed the studies. Dr. W. H. Burt of the University of Michigan has given many helpful suggestions. Dr. D. L. Allen, then Biologist in charge at the Swan Creek Wildlife Experiment Station, contributed many field records and valuable field supervision. The United States Department of Agriculture and Works Progress Administration did considerable developmental work on the study areas. The cooperation of F. J. Hodge, then in charge of the wildlife developmental work for the United States Department of Agriculture, is appreciated.

Betty M. Robertson of the University of Michigan Department of Botany identified the plants collected during the study. Identification of several parasites has been made by Dr. J. C. Bequaert of Harvard University, Dr. H. E. Ewing of the United States Bureau of Entomology, and Drs. S. C. Whitlock and Carl Gower of the Michigan Department of Conservation Pathology Laboratory. Many valuable field records were contributed by F. W. Stuewer, R. C. Dunning, P. S. Baumgrass, J. D. Cameron, and W. T. McConnell.

Area Studied

The major portion of the present study was made on parts of 10 sections of land on or near the Swan Creek Wildlife Experiment Station, Allegan County, Michigan. These sections were 5, 8, 9, 17, 21 and 28 of Valley Township, sections 31 and 32 of Heath Township, and sections 11 and 12 of Clyde

¹ Extraction from a dissertation submitted in partial fulfillment of the requirement for the degree of Doctor of Philosophy, in the University of Michigan. *Part 2*

Township, all of Allegan County, Michigan. The major portions of the investigation were made in upland habitats which lie within half a mile of fertile lowland areas. Many records, however, were secured in riverbottom habitats.

PHYSIOGRAPHY AND SOIL

The surface area is generally flat (650 feet above sea level), with only a few minor irregularities. The Kalamazoo River cuts through the sandy upland plain in the form of a wide meandering valley with extensive bayous. Abrupt escarpments which rise up to 50 or 60 feet in a few places separate the upland from the riverbottoms.

The soil consists of Plainfield Sand (formerly known as "Allegan Sand") which is very deep, sections of 30 to 60 feet being recorded (Fippin and Rice, 1901). Only a small amount of organic matter is found in the thin sandy loam surface layer of soil. According to Veatch (1933), the land is of third class, which is in general submarginal, or locally marginal.

CLIMATE

The annual precipitation in Allegan County is about 30 inches. Included in this amount is an annual snowfall of 60 inches (Fippin and Rice, 1901). The mean temperature for the county is about 48 degrees Fahrenheit, the average annual maximum 95.9 degrees, and the average annual minimum minus 12.1 degrees Fahrenheit. The average length of the crop growing season is about 160 days (Leverett, 1917). During 1938 and 1939 the weather was not unusual.

VEGETATION

The present woody vegetation on the sandy upland plains consists almost entirely of oaks (*Quercus alba* and *Quercus velutina*) ranging in size up to about 10 inches in diameter at breast height. A moderate amount of sassafras, cherry, and dogwood is found amongst the smaller ground cover. The deserted farm lands are slowly being invaded by weeds, dewberry, sassafras, cherry, and oak. A few of the old fields, however, have large patches of "blow sand" which have been partially put under control by soil conservation measures.

With the advent of fall frosts, the leaves of most shrubs and trees are dropped. Most white oaks and much of the black oak coppice and reproduction, however, do not drop their leaves until after the snow has disappeared the following spring (Fig. 1).

OCCURRENCE OF HOLLOW TREES AND BURROWS ON UPLAND

A few (about 1 per 20 acres) of the oak trees on the areas have small hollows in their bases. Such holes, where they occur, are readily used by rabbits. Hollow pine logs are used occasionally, but their scarcity (about 1 per 40 acres) limits their usefulness. Woodchucks and skunks are seldom found on the upland, and accordingly, their burrows are usually lacking. A badger or family of badgers which were occupying one or more of the study areas, were not known to use more than three or four burrows. Apparently, the

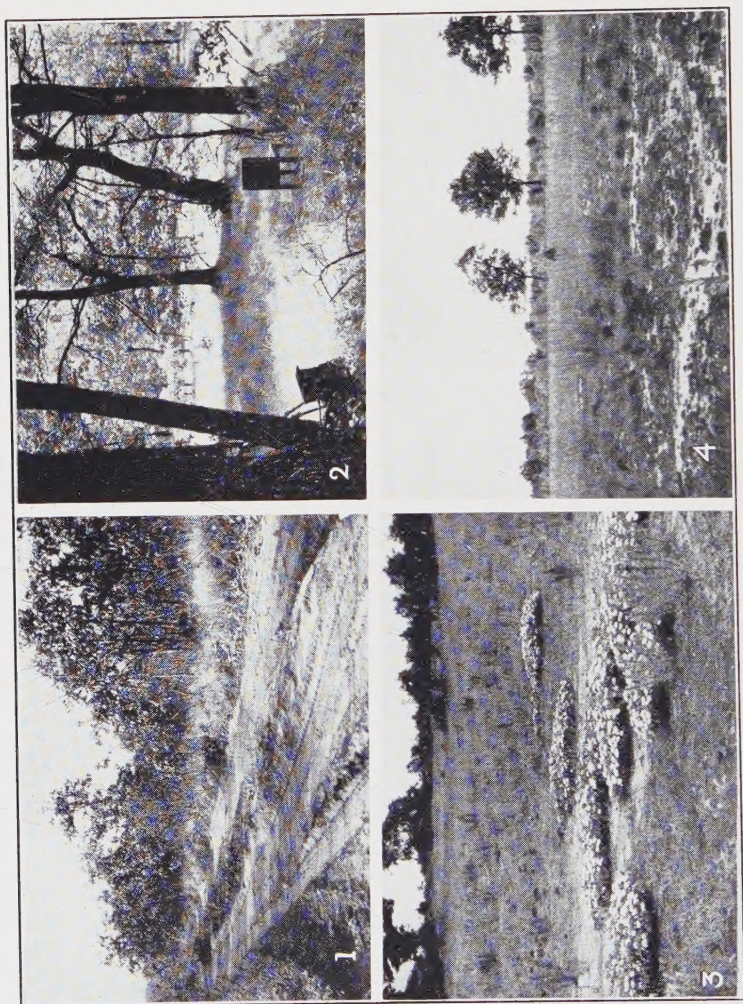


Fig. 1. Good cottontail cover. Fig. 2. No rabbits were taken at this trap station during two years of study. No suitable cover for rabbits present. Fig. 3. One of the largest beds of cactus in the region. Fig. 4. Destruction of the natural cover caused this "sand blow," which is now healing over.

scarcity of ground squirrels provided little opportunity for badgers to dig in pursuit of such prey. A few of the upland sites are lacking in suitable winter cover (burrows, brush piles, coppice) and consequently the rabbits migrate from those areas into the bottomland during that season (Fig. 2).

Methods of Study

Information about the cottontail has been secured by live-trapping, shooting, examining dead individuals from roads, examining burrows, tracking, scatology, and direct observation.

TRAPPING TECHNIQUE

Spacing of traps.—Forty-nine permanent trap stations were established in each of the six 160-acre areas studied. These trap stations were located at 110-yard intervals and arranged in a grid pattern. Outside rows of traps were located 110 yards inside the border of the areas. Trap stations were numbered in consecutive order, and a metal tag stamped with the quadrat and trap station number was nailed to a nearby tree or post.

Each of the traps was set near the most suitable cover available within 50 feet of the established station. The most suitable place was usually at the base of a clump of bushes or near the base of a tree. Traps were usually placed with their entrance directed toward cover. During summer, traps were placed where they would be shaded during the forenoon, because continued exposure to hot summer sunshine is fatal to cottontails.

Traps.—A trap similar to the "Evans vermin trap" (McAtee, 1930, Fig. 2) has been effective for live-trapping cottontails. A suitable size for such a trap is 12 inches high, 12 inches wide, and 24 inches long.

Baits.—A combination of plain ear corn, or corn soaked for 2 or 3 days in a salt solution, and rolled oats or apples has proved to be effective bait for cottontails. Combinations of these baits have attracted rabbits at all seasons. A large number of additional baits were tried at times, but these did not show any promising results. These additional baits tried were commercial cow feed, whole oats, scratch feed, commercial rabbit pellets, alfalfa, shredded Ralston cereal, carrot, radish, turnip, beet, parsnip, raisins, catnip, pennyroyal, mint, and vanilla. Smoked herring was often placed along with other baits in the traps in order that the catch of raccoons might be increased.

Cottontails do not react in the same manner to baits at all times. One night the rabbits may run directly past a trap without hesitation. On another night, they may pack the snow down all around the trap, but will not enter. At still other times, they enter the traps freely.

Tending traps.—Traps were visited during the forenoon of each day. Whenever two or more traplines were operated simultaneously, some traps could not be visited until about noon.

Handling rabbits.—Rabbits were removed from traps in the following way: the trap was set on end, then the operator reached into the trap and seized the rabbit from above. The struggles of the rabbit were least successful when it was seized about the neck with the thumb and index finger, and the little finger hooked around the hind foot, which was then brought forward (Fig. 5). When a rabbit was held thus, it made little attempt to kick with the other hind leg, and was never injured. The rabbit was then placed into a small cloth bag where it was examined for sex, age, ectoparasites, and general condition, its hind foot and ears measured, and its weight taken. If the rabbit was an adult female, it was examined for signs of lactation and pregnancy. Measurements were taken of the length of testes of males. Rabbits which were taken for the first time were marked by attaching consecutively numbered tags to their ears. Males were tagged on the right ear and females on the left. The tag numbers of rabbits which had been marked previously were recorded with the other data taken.

During summer and fall of 1939, rabbits were tagged in both ears as an insurance against loss of identity with loss of ear tags. Both button type and fingerling tags were used (Figs. 6 and 7). Fifteen tags were known to have been lost during 1938 and 1939. Apparently, both types of tags are sometimes torn from the ear. The fingerling tag is probably the least susceptible to loss if properly attached to the ear. The most satisfactory way to attach fingerling tags to a rabbit's ear is to insert it through the back side of the ear at 2 places arranged in a proximal-distal direction (parallel to axis of ear, Fig. 7).

Tracking.—Tracking in a fresh snow has proved to be an excellent means of determining the range of activity of rabbits. The extent of use of artificial food, artificial burrows, and brush piles has been effectively determined by tracking. On several occasions, tracking showed the absence of cottontail activ-

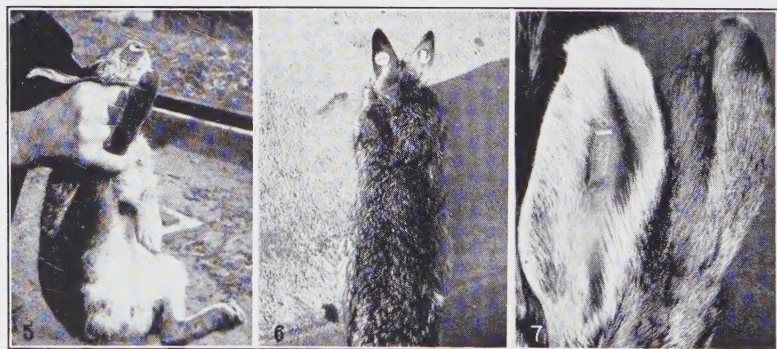


Fig. 5. A safe, painless, and easy way to handle a cottontail. Fig. 6. A cottontail which has been marked with a numbered button-type ear-tag in each ear. Fig. 7. Cottontail marked with numbered fingerling-type ear-tag. Photo by L. C. Hulbe t.

ity in one area, when an abundance of rabbit activity was found in more suitable areas.

On a few occasions, a colored paste prepared from methlyn blue, glycerine, and flour was smeared on the feet of live-trapped rabbits. The color left in the tracks served as an aid in tracing range of activity. The preparation rapidly lost its value for coloring the foot prints, but did last for 12 hours if the snow was wet.

Scatology.—The fecal pellets of rabbits serve as an index to the use of brush piles. The presence of large numbers of fecal pellets along the perimeter of brush piles indicates that cottontails spend considerable time sitting in the edge of such cover. In late winter of 1938, one large brush pile contained an average of 48 fecal pellets per foot of perimeter, or edge of the pile. Several nearby brush heaps were used almost as intensively.

Various harmless stains were given to a few rabbits to color the feces and urine. The colored urine and fecal pellets were then used as clues in studying the home range of individuals treated. Blackish pills resulted from the forced feeding of charcoal. Methlyn blue colored the pills green, and the urine a bluish green. Reddish saffranin colored the urine reddish, and the pellets a pinkish brown. Alphazurine stained the pills a brilliant green color which was recognizable at a distance of 8 to 10 feet. Gentian violet and acriflavine stains were unsatisfactory. These stains were administered by placing them in small gelatine capsules which were then forced down the throat of the rabbits.

Life History

A sound management plan for any species must consider its needs as exhibited by its everyday habits and life processes. Accordingly, I have endeavored at all times to gather all available information relative to the life history of the cottontail.

GENERAL BEHAVIOR

Fear.—Cottontails lose some of their fear of man when they are recaptured frequently. The first time they are taken, they usually batter themselves against the wire of the trap. On subsequent captures, however, they remain more quiet at the approach of the operator. A few rabbits which were brought into close proximity with weasels, skunks, and opossums did not show much fear until attacked. If the attack occurred in a burrow, as described elsewhere in this paper, the immediate reaction was to dash from the burrow, even when the only exit was past the attacker. Captive rabbits, however, were much frightened at the approach of a dog.

Defense.—A mature rabbit is far from defenseless. Its powerful hind legs are deadly weapons. During the first year of study, the writer's hands were constantly scratched until he learned how to seize and hold a rabbit properly (Fig. 5). Captive rabbits proved to be especially difficult to handle. When an attempt was made to grab them, they usually attempted to elude capture, but when cornered they became aggressive and fought. These captives defended

themselves by stabbing with the front feet, and then suddenly lashing forward with both hind feet. When confined in a bag, they would sometimes bite. One rabbit when attacked by a skunk in a burrow seemed to lie back on the dorsal part of its rump and to thrash the skunk with its powerful hind legs.

Voice.—Ordinarily, a rabbit does not use its voice, but when seized and lifted into the air, it may utter a high-pitched rasping sound. On a few occasions, while young rabbits were being taken from a nest, they uttered this call. The other young left the nest immediately and scattered, so the call in this case served as an alarm.

Sociology.—Eight pairs of rabbits were kept in small pens (3 x 5.5 feet) during the summer and fall of 1939. The claws of one pair, which fought considerably during their first night together, were cut short and blunt. No serious fighting occurred after this treatment, and no fatalities occurred. Some of these rabbits had been reared in captivity, while others were taken from the wild. Several wild-caught rabbits have been kept over night in a single compartment without fatalities. These wild rabbits seemed more tolerant toward each other than cottontails are usually reported to be.

Rabbits have on several occasions been taken in pairs at a single station during the breeding season, when two traps were operated at the stations. This apparent companionship was evidently due to sexual instincts.

On one occasion an adult male in breeding condition was taken in the same trap with an immature female which weighed only 14 ounces. Perhaps then there is some companionship between juvenile and adult rabbits.

WINTER FOOD ON UPLAND

During the winter, cottontails occupying the sandy upland usually made use of the foods which were most available. Bark, twigs, and buds of white oak,

TABLE 1.—Plants used for food by cottontails on upland study areas, during winters of 1937-38 and 1938-39. Listed in order of importance as food.

SPECIES	AVAILABILITY	USE
<i>Quercus alba</i> (White oak)	abundant	frequent
<i>Cornus florida</i> (Flowering dogwood)	common	frequent
<i>Sassafras albidum</i> (Sassafras)	common	frequent
<i>Quercus velutina</i> (Black oak)	common	frequent
<i>Ceanothus americanus</i> (New Jersey tea)	common	frequent
<i>Pinus Strobus</i> (White pine)	common	less frequent
<i>Smilax</i> sp. (Greenbrier)	occasional	less frequent
<i>Rubus procumbens</i> (Dewberry)	abundant	less frequent
<i>Pyrus malus</i> (Apple)	occasional	less frequent
<i>Pinus Strobus</i> (White pine)	occasional	infrequent
<i>Vaccinium</i> sp. (Blueberry)	occasional	infrequent
<i>Crataegus</i> sp. (Hawthorn)	occasional	infrequent
<i>Populus alba</i> (Silver-leaved poplar)	scarce	infrequent
<i>Rosa</i> sp. (Rose)	occasional	infrequent
<i>Artemisia caudata</i> (Wormwood)	abundant	infrequent
<i>Gaylussacia baccata</i> (Huckleberry)	occasional	infrequent
<i>Gaultheria procumbens</i> (Teaberry)	local	infrequent
<i>Hamamelis virginiana</i> (Witch-hazel)	common	infrequent

flowering dogwood, sassafras, and New Jersey tea were taken in liberal amounts in the order listed (Table 1). Black oak was similarly used, but the buds were cut from the twigs and rejected. It was rather common to find a group of black oak buds lying where a rabbit had been feeding on the twigs of that species. Wormwood (*Artemisia caudata*) which grows in abundance on the areas was apparently not taken for food as frequently as its availability permitted. Wild black cherry, greenbrier, dewberry, and apple, were used only in moderate amounts. Lack of availability was probably the limiting factor in the infrequent use for food of such plants as white pine, blueberry, hawthorn, silver-leaved poplar, rose, huckleberry, teaberry, and witch-hazel.

The list of foods used by the cottontails (Table 1) is not intended to represent all foods taken on the upland during winter. However, it does contain all important foods, as well as a few lesser important ones.

REPRODUCTION IN THE COTTONTAIL RABBIT

In spite of the fact that the cottontail rabbit is one of our most important game species, accurate information relating to its breeding season has been inadequate. Data relating to the breeding of this animal seem to have been chiefly secured through autopsies, from the absence or presence of signs of lactation in dead females, nests of young, and from observations on mating behavior. Trippensee (1934) noted the annual increase and decrease in size of testes in the males, the presence of embryos in autopsied females, and nesting habits, and deduced from this evidence the breeding season.

This method of approaching the problem is undoubtedly sound, except that the amount of evidence to be secured by such a means is obviously limited, because the season for legal take is usually closed when the rabbits are breeding, and the nests are almost invariably discovered by accident. Beule (1940), however, has had considerable success at finding nests by a systematic search. Only one of the eight nests examined by me was found by intentional search.

Method of securing data on reproduction.—The present study differs from those of the past in that, in addition to nest and autopsy data, living wild female rabbits were periodically examined for signs of pregnancy or lactation, and males for size of testes.

Diagnosis of pregnancy.—The presence of uterine swellings, or large embryos in a living female cottontail was determined by gently pinching the walls of its abdomen together between the thumb, index, and second fingers. If the investigator is careful, fecal pellets, kidneys, uterine swellings, and occasionally a dilated bladder can be distinguished. Until one has had some practice with this technique, he may confuse parts of the rabbit's internal anatomy. However, with a moderate amount of effort and patience, he soon learns to diagnose a case of pregnancy which is sufficiently advanced to show uterine enlargements. Obviously, swellings of the uterus cannot be measured, therefore, they were classified as approximately the average size of a (1) cottontail fecal pellet, (2) hazelnut, (3) hickory nut, (4) or walnut. Swellings larger than a walnut were considered as evidence of an advanced stage of pregnancy. Preg-

nancies in which the uterine swellings were approximately the size of a fecal pellet usually were questioned, and later verified when the rabbit was recaptured and found to have uterine swellings of increased size.

The age of one embryo which was secured from a 14-mm. uterine swelling in a wild cottontail has been determined by Dr. A. H. Stockard, of the University of Michigan, to be about 12 days. Such a uterine swelling (14-mm.) when palpated in the abdomen of a live rabbit feels comparable in size to a large hazelnut.

Measuring testes.—The method used for measuring the combined lengths of a testis plus its epididymus, while still in the scrotum of a living rabbit, was to gently force the testis into the bottom of the scrotal sac by means of the thumb, index, and second finger of the left hand, and then measure the organ with a 6-inch ruler held in the right hand. This procedure can be employed with a minimum of struggle on the part of the rabbit, if its hind quarters are protruding from a closely fitting cloth bag, while the rabbit is lying on its back, head facing the left, on the lap of the observer. Since only a close approximation of the actual size of testes could be obtained by this method, the measurements were read to the nearest one-fourth inch, except in those instances where the measurements fell exactly on a one-eighth inch mark.

The testes of dead rabbits were removed from the animal before being measured. Only a single measurement was taken, the maximum length of the testis, exclusive of the part covered by the epididymus.

Gestation.—Dice (1929, 1933) found that an experimental mating of a pair of rabbits (*Sylvilagus f. alacer*) in captivity produced a litter of three young, which were found on the 28th day after mating, but explains that the litter may have been present before he found them. Hammond (1931) has found in the "domestic rabbit" that "... the mean duration of pregnancies is very slightly under 32 days, and that 95 per cent of the pregnancies lie between 30 and 34 days."

Evidence on length of gestation period in wild cottontails.—Eleven females were handled repeatedly in one quadrat during the breeding season of 1939. Four of these were retaken at times when they were apparently undergoing a subsequent gestation period with embryos comparable in size to those observed in an immediately previous pregnancy of the season. One of these females was found in the advanced stages of three separate pregnancies during the 1939 season. The number of days which elapsed between apparently similar stages of development in successive pregnancies of individual females are presented in Table 2. Female No. 17 was taken twice, 34 days apart, and contained advanced embryos of about equal size on these occasions. Thirty-one and 32 days after rabbit No. 941 was observed in an advanced stage of pregnancy, she was found to have uterine swellings of walnut size, and on the 67th day she was again in an advanced stage of pregnancy. This female, therefore, must have completed gestation of the embryos which were of walnut size, and barring abortion, must have given birth to her young, again become pregnant, and undergone gestation of a succeeding litter (2nd) to an advanced stage, all in

a period of 35 days. A third female (No. 946) showed two advanced stages of pregnancy only 26 days apart. On June 15 and 17, and again on July 14, female No. 61 was recorded as pregnant with embryos about the size of a walnut. The minimum time between handling this female was 27 days, and the maximum time 29 days. A female handled repeatedly on another area required 19 days for its uterine swellings of hazelnut-size to develop into embryos which would probably be born within a day or two.

TABLE 2.—Time Interval Between Comparable Stages of Succeeding Pregnancies of Individual Female Cottontail Rabbits.

Animal Number	Date of original observation	Days until succeeding comparable size of embryos	Days until third comparable size of embryos
17	May 20	34	
61	June 15	27-29	
941	April 24		67
946	May 2	26	
Average No. days interval		29.3	67

It is recognized that the time between the various designated stages of pregnancy is probably not constant, and that a diagnosis of a given stage of pregnancy is only an approximation, which may vary 4 or 5 days in its accuracy. However, female No. 941 more than completed the cycle from one litter to the next in 35 days. The gestation period for this species is therefore less than 35 days, and may be as low as 26 days. Hammond and Marshall (1925) found that "while it is a rule in the rabbit that pregnancy does not occur during lactation, there are two circumstances under which it is possible: (a) where only a small number of young are being suckled, and (b) in times of abundant nutrition suitable for breeding." Vorhies and Taylor (1933) in working with *Lepus alleni* and *L. californicus* found that "pregnancies frequently occur while young are being suckled. . . ." Therefore, if copulation and resultant fertilization follows parturition immediately, then the gestation period of *Sylvilagus f. mearnsii* is less than 35 days and probably more than the indicated 26 days minimum. Gerstell (1937b) found in captive rabbits ". . . that births occurred any time between 25 and 32 days after copulation, the normal period of gestation apparently being 30 days." Some variation in length of the gestation period is to be expected. Hammond and Marshall (1925) observed that the duration of 95 per cent of the pregnancies in the domestic rabbit did not vary more than 4 days, and that ". . . there is only a suggestion that the duration of pregnancy, when it occurs, has been slightly prolonged by increasing the number of young suckling; the limits, however, do not exceed the normal variation."

The average length of time between comparable stages of pregnancies in a single female, as based on evidence from four individuals, is 29.3 days. The average gestation period is, therefore, probably about 29 or 30 days.

Number of litters.—Dice (1929, 1933) succeeded in rearing, in one season, two litters of young from a pair of captive rabbits (*Sylvilagus f. alacer*). Trip-

pensee (1936) states that "no direct evidence has been obtained on the number of litters in southern Michigan." Allen (1938b) says, "If the gestation period of the cottontail is roughly one month and the young are cared for by the mother for 16 (or a few more) days, 50 days would encompass the length of time needed for producing a litter." On the basis of this calculation, Allen indicates that probably only two litters are ordinarily produced in a season.

Evidence on number of litters borne during one season.—The number of litters an individual female cottontail may bear during a single season has been determined for five females (Table 3). These females were recaptured frequently during the intensive study of a sample area (160 acres) in 1939. Intensive trapping operations within this area were conducted as follows: April 13-May 6, May 24-29, June 27-July 3, and from August 5 to September 18, 1939. Nine adult females were taken during April 13 to May 6. Some females were not retaken during subsequent censuses, others were not recaptured until the third or fourth recensus was taken. Only two additional individual females were taken as the season progressed.

If the mammae of a rabbit contained milk, or if the hair about the nipples

TABLE 3.—Frequency of Pregnancies Among Female Cottontails Taken on a Sample Area.

Date	Female number									
	17	134	163	491	500	504	821	941	946	951 1011
April 1-10	..	..	..	..	..	..	..	..	..	..
11-20	L1	L1	A1	L1	P1	..	L1	L1F2	A1	..
21-30	Hc2	Hc2	..	..	..	..	..	A2	..	F1
May 1-10	..	..	..	..	..	L1Hz2	..	..	Hc2	L1
11-20	..	..	..	..	..	..	..	..	..	..
21-31	A3	W3	F2	..	..	F3	..	W3	Hz3	L1A2
June 1-10	..	..	..	..	..	..	..	..	..	..
11-20	..	..	..	..	..	..	..	..	..	..
21-30	A4	..	..	..	..	Hz4	..	A4	..	..
July 1-10	..	..	..	..	..	..	..	..	..	..
11-20	..	..	..	..	..	..	..	..	..	..
21-31	..	..	..	..	..	L	..	..	..	..
August 1-10	..	..	..	..	..	..	..	..	..	L
11-20	..	..	..	..	..	..	..	L	..	LHz3
21-31	..	..	..	..	L2	L	..	..	L4	..
Sept. 1-10	..	..	..	..	..	L	..	..	..	..
11-20	..	..	..	..	..	..	..	..	..	..
21-31	..	..	..	..	..	..	..	..	..	..
Apparent no. times pregnant	4	3	2	1	2	4	1	4	4	1 3

Key: Sizes of Pregnancies—1, 2, 3, 4,—first, second, third or fourth pregnancy

F—fecal pellet

A—advance

Hz—hazelnut

P—size unknown—no observation

Hc—hickorynut

L—lactating (at least 1 litter born)

W—walnut

was matted when examined, it was considered that the rabbit had given birth to a litter. Hammond (1931) found in the domestic rabbit that "from about the 20th day onwards the mammary gland begins to undergo its thickening or alveolar glands stage of growth (felt as a thickening when the skin is held between the finger and thumb—an indication of pregnancy)." Until the time when such a change in the mammary glands takes place, it is reasonable to suppose that a rabbit cannot lactate. Therefore, a rabbit found lactating, and at the same time carrying embryos no larger than a walnut, was considered to be in at least its second pregnancy for the season.

It is evident that if an individual was handled approximately once each month, the number of pregnancies during a single season could be determined. Trapping on the sample area was not begun, however, until about a month after the advent of the breeding season.

Five of the females examined had apparently completed their first pregnancy of the season prior to the middle of April, as they were lactating at the time (Table 3). Three of the 11 does handled on the sample area during the breeding season, were apparently pregnant once; 2, twice; 2, three times; and, 4, 4 times. Two of the three which were found pregnant only once, were not retaken, and hence are not completely accounted for. The third female (No. 821) with only one observed pregnancy, was repeatedly retaken on a distant area during July. She was neither pregnant nor lactating. This female should probably not be considered as normal because she was "stocked" onto an adjoining area on January 26, 1939. At that time she was released in an unoccupied locality where a female of the same age had perished. However, she seemed inclined to roam, with no apparent fixed home range. Both animals which were twice found pregnant were not retaken a sufficient number of times to allow a determination of the complete number of pregnancies. Each had ample time to breed three or even four times during the season. Female No. 500, which was found pregnant in April, was not retaken until late August at which time she was lactating. Therefore, it seems reasonable to assume that she had given birth to at least two litters during the season. Rabbit No. 134, which in late May was pregnant for the third time, was not retaken thereafter.

Under favorable conditions, pregnancy does occur in the "domestic rabbit" during lactation (Hammond and Marshall, 1925). They likewise found that a high percentage of fertile coitions occurs during the first four days after parturition. Vorhies and Taylor (1933) found that in the jack rabbit *Lepus alleni* and *L. californicus*, "pregnancies frequently occur while young are being suckled. . . ." In general then, it seems that the four pregnancies indicated by four of the 11 females taken on this sample area were not unusual for the region.

None of the rabbits handled were found pregnant during the same year in which they were born. Females of *Sylvilagus audubonii audubonii*, however, do mature and bear young during the same year (Ingles, 1941).

Testes.—Trippensee (1934) found that the size of the cottontail testes began to increase in early December, reached a maximum in April, and was

sharply reduced during the latter part of July and August. His findings are based on relatively few measurements, most of which were evidently taken during late fall months. Early in the present study, it was realized that if a series of seasonal measurements could be taken on the testes of a single individual, much could be learned about the duration of the reproductive season.

The testes (in scrotum of living rabbits) in 87 adult and 89 juvenile cottontails were measured a total of 246 and 143 times, respectively, during 1938 and 1939. In addition, 28 adult and 18 juvenile male rabbits were autopsied, and the testes measured after they were removed from the scrotum. This autopsy measurement is the distance from the opposite ends of the testis, excluding the part covered by the epididymus. Testes measured after they were removed from the scrotum have usually been of a size intermediate to the extremes of the sizes found by simultaneous measurements on a number of live rabbits. The apparently close correlation in sizes of testes found by the two non-comparable methods may be due to a slight compression of the testis and its epididymus as they are gently forced into the bottom of the scrotum to be measured. Size of testes as determined by periodical measurements on live rabbits, and from autopsies, have been grouped together to show the trend of seasonal changes in testis size of cottontails (Table 4).

Seasonal fluctuations in testis size of adults.—The testis size rapidly rises during January, February, and March, then increases more slowly to a high level in April and early May (Graph 1, Fig. 8). Decline in size is rather slow during June and most of July, but drops off rapidly in late July and August (Fig. 9). By the middle of September, the size of adult male testes has fallen to about 1.1 inch, at which size they apparently remain until December (Figs. 10 and 11). The decrease in average size to 1.0 inch during late October is only 0.1 inch smaller than the average for the other fall periods, and is probably not significant.

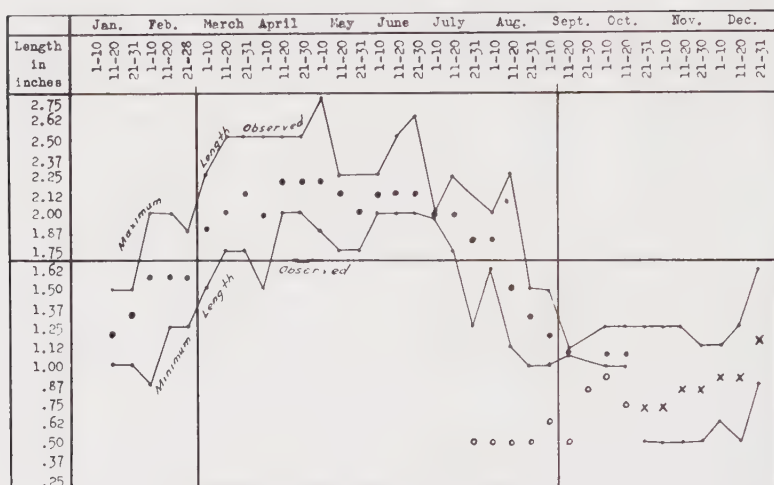
Increase of testis size in juvenile rabbits.—The testes of living juvenile rabbits cannot be measured in the scrotum satisfactorily until the animal is about a third grown, and then only with difficulty. Measurements of the testes of juvenile rabbits were first secured in July, at which time they averaged one-half inch in length. From this time on, the size of testes increased, with some apparent fluctuations, until mid-December, when they were 0.9 inch long. Until about October 21, juvenile and adult male cottontails could be distinguished on the basis of testis size (Fig. 11). From this time onward, however, a small amount of overlapping in range of sizes occurs. Therefore, after the middle of October, it is advisable to treat all males as one group of potential breeders. The average testis size for such a group is given in Table 4.

Breeding season.—Trippensee (1936) says, "Observations in the field indicate that there is a definite breeding season for the Mearns cottontail beginning in the middle of January and extending to the middle of August." Allen (1938b) states that the regular breeding season lasts from February through July, although some breeding evidently occurs earlier and later than this.

In my study, the rabbits examined prior to March 14 were apparently not

TABLE 4.—Summary of Data on Cottontail Rabbit Breeding Season, 1938, 1939.

Period of month by ten-day intervals	Males							Females		
	Adult			Juveniles			Mean length of testes in combined age classes	Adult		
	Mean length of testes in inches	Number individuals	Number measurements	Mean length of testes in inches	Number individuals	Number measurements		Individuals pregnant	Individuals lactating	Individuals not pregnant
Jan. 1-10		0	0					0	0	ALL
11-20	1.2	4	8					0	0	ALL
21-31	1.3	5	5					0	0	8
Feb. 1-10	1.6	16	20					0	0	6
11-20	1.6	13	22					0	0	2
21-28	1.6	6	10					0	0	1
Mar. 1-10	1.9	17	21					0	0	4
11-20	2.0	15	16					3	0	7
21-31	2.1	15	16					5	0	7
Apr. 1-10	2.0	11	12					4	0	2
11-20	2.2	17	22					12	13	2
21-30	2.2	5	5					4	7	2
May 1-10	2.2	7	9					4	10	1
11-20	2.1	12	14					9	9	0
21-31	2.0	6	6					14	15	3
June 1-10	2.1	2	2					4	4	0
11-20	2.1	6	7					6	10	1
21-30	2.1	8	10					3	10	3
July 1-10	2.0	1	1					1	3	2
11-20	2.0	2	2					4	4	11
21-31	1.8	13	22	0.5	1	1		9	17	10
Aug. 1-10	1.8	8	9	0.5	4	4		2	8	5
11-20	1.5	3	3	0.5	3	3		1	4	4
21-31	1.3	7	10	0.5	5	5		0	6	5
Sept. 1-10	1.2	2	4	0.6	6	7		0	9	11
11-20	1.1	1	1	0.5	5	6		0	2	1
21-30		0	0	0.8	3	4		0	0	ALL
Oct. 1-10	1.1	2	2	0.9	1	1		0	0	ALL
11-20	1.1	2	3	0.7	4	4		0	0	ALL
21-31	1.0	7	8	0.7	21	36	0.8	0	0	ALL
Nov. 1-10	1.1	3	3	0.7	28	28	0.7	0	0	ALL
11-20	1.1	4	4	0.8	26	32	0.8	0	0	ALL
21-30	1.1	2	2	0.8	10	15	0.8	0	0	ALL
Dec. 1-10	1.1	2	2	0.8	4	5	0.9	0	0	ALL
11-20	1.1	3	3	0.8	11	11	0.9	0	0	ALL
21-31	1.2	8	8		0	0	1.2	0	0	ALL



Graph 1. Annual change in length of cottontail rabbit testes. Curve based on data from Table 4. Key: • Average length of adult testes; ○ Average length of juvenile testes; × Average length of juvenile and adult testes.

pregnant. On March 14, 1939, however, three of the six females taken had small uterine enlargements. From this date on, pregnancies were frequent. Signs of lactation were first found on April 11. Evidence of breeding (pregnancies or lactation) was found throughout April, May, June and July. The last pregnancy of the season was found on August 11, at which time this female had uterine swellings about the size of a hazelnut. She was probably destined to bear young some time in late August or early September.

On September 12, 1939, a nest with young was reported to have been found by a farmer near Dorr, Michigan. The report was checked by me and the deserted nest located. At least three farmers saw the young, whose eyes were open, run from the nest when disturbed. Allen (1938b) found evidence indicating that the eyes of a litter under observation opened on the eleventh day, and that the young left the nest on the 16th day. It is accordingly probable that the young rabbits in the nest on September 12 were born some time between August 27 and September 1.

Evidence of lactation continued to be found until the middle of September. From this time on, all females examined were without signs of either lactation or pregnancy (Table 4).

The term "breeding season" as used here refers to the length of time between the first fertile coitions of the season, and the time when the last young of the season are capable of independent existence. Hamilton (1939) states that "the season for reproduction is normally considered to be that period when adult animals are concerned with mating and the care of young." The cottontail, as previously shown, normally mates and cares for 3 or 4 litters each year in southern Michigan.

The early March beginning of the breeding season agrees with the observations of Allen (1938b), but is about a month and a half later than was indicated by Trippensee (1936). The season comes to a close in September, and in this respect agrees most closely with the evidence of Trippensee. Although the number of my records is not large, they are scattered evenly throughout the year, so chances for observing the absence or presence of signs of breeding were favorable. The breeding season began suddenly and continued until the last young were weaned about the middle of September. It therefore appears that rabbits in this region have about a six-months' breeding season, starting early in March and extending to early or middle September. Fertile coitions were accordingly made during the period between early March and the middle of August, during which time the testes of males averaged 1.8 inches or more in length.

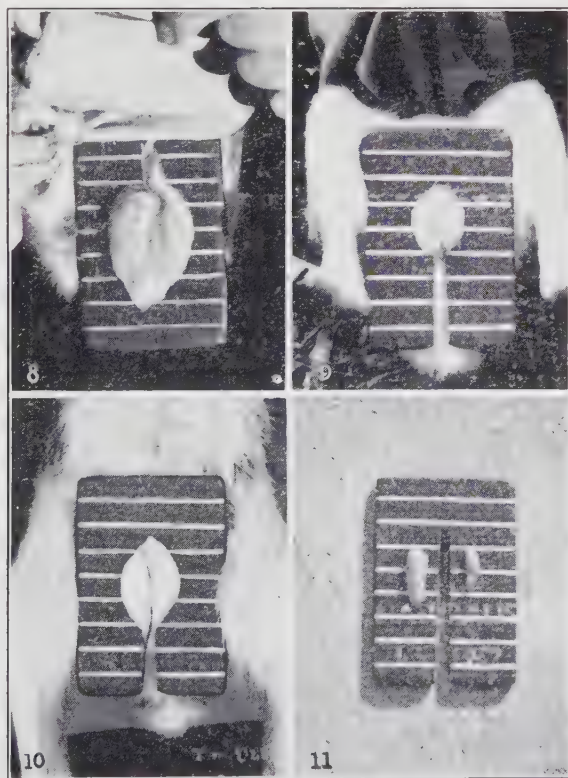


Fig. 8. Size of testes of cottontail on April 23, 1939. Fig. 9. Size of cottontail testes on August 17, 1939. Fig. 10. Size of cottontail testes on December 14, 1939. Fig. 11. The testis on the left is that of an adult; that on the right is from a juvenile. December 14, 1939.

Number of young per litter.—The average size of 12 litters of young observed during 1938 and 1939 was 5.4 (Table 5). A nearly similar average of 5.42 was found by Beule (1940) in Pennsylvania. Allen (1938b) found that evidence from nests and autopsies in Michigan indicated an average litter size of 5.1 young. Trippensee (1936) compiled the data given by several workers in Michigan and calculated that on the basis of 27 litters, the average was 5.04. My data on the average size of litters were secured through autopsies on 5 pregnant females, observations on 4 nests and three litters born in captivity. Differences in average size of litters as determined by these workers and by my study are not significant.

Nesting and care of young.—Only eight cottontail nests were examined during the two years of study. Six of these still contained young when found, but two were empty at the time visited. The young from two others were removed to the experiment station for later study. The two remaining nests, Nos. 1 and 3 of Table 6, were frequently visited to weigh, measure, and photograph the young, some of which were ear-tagged.

Six of the nests examined consisted of a bowl-shaped excavation in the ground; a seventh was shaped similarly, but was formed above ground in a 6-inch bed of straw. The cavity of a nest is sometimes a trifle larger than, and slightly to one side of the top opening. At no time was a nest excavated in the ground in such a way that a tunnel was necessary to reach it. The average size as determined from measurements of four nests is: length of opening, 6.4 inches; width of opening, 4.7 inches; and depth of excavation 3.3 inches. They have been variously lined with rabbit fur, fine grass, and short pieces of grass stems which the rabbit had apparently cut. However, only a faint indication of hair was found lining the nest formed in a bed of straw. Nests containing young were covered with a concealing mat of rabbit hair and grasses. This mat, however, with use, or when tampered with, seems to become partly damaged or destroyed.

TABLE 5.—Records of Cottontail Litters Obtained from Nests, Autopsies, and Births in Captivity.

DATE	NO. OF YOUNG	SIZE	EVIDENCE
3/21	5	24.5 mm.	Embryos
3/23	4	3.5	Embryos
4/9	4	117.5	Born in captivity
4/11	6	---	Nest
4/18	4	105.0	Embryos
4/18	7	22.5	Embryos
4/26	7	---	Nest
5/10 and 11	5	115.0	Born in captivity
5/29	6	112.0	Born in captivity
6/8	5 (?)*	---	Nest
7/25	6	56.0	Embryos
7/31	6	---	Nest

Total young in twelve litters—65.

Average number—5.4.

* A dog had taken 2 of the 5 young before I examined the nest.

TABLE 6.—Location of Cottontail Nests.

NEST NUMBER	LOCATION	COVER	TERRAIN	CLOSEST ESCAPE COVER
A	Grassy field	Weeds	Flat	?
1	Field	Stump	Flat	25 yards
2	Dike bank	Tree	Bank	Immediate
3	Orchard	Bed of straw	Flat	9 yards
4	Field	Stubble	Sloping	?
5	Alfalfa field	Alfalfa	Flat	Immediate
6*	Alfalfa field	Alfalfa	?	Immediate
7	Corn field	Hill of corn	Flat	Immediate

* Not examined by me.

There was no indication that the doe deserted the young in any of three nests in which young were frequently handled. Five days previous to my visit, one nest had been raided by a dog, which took two of the five young. The remaining three were apparently still in good condition when examined. It is doubtful if these young could have survived for five days without their mother's care, as their eyes were not yet open when first disturbed. It was on the fifth day after their eyes opened that the three survivors, which were placed in captivity, were first seen to eat grass. According to Allen (1938b), they were about 16 days of age at this time.

Nest No. 1 was found in a slight concavity against the base of an old stump standing in an open field (Table 6 and Fig. 12). When the nest was disturbed, 6 squealing young scattered in various directions. They were captured, their sex determined, and all but one replaced in the nest. The 4 females and 2 males had their eyes open and were probably about 14-15 days old. The one individual kept captive weighed 74.34 grams, its hind foot measured 38.5 mm. and its ear measured 25 mm. A few hours later that same day, only one male remained in the nest. It was then ear-tagged. Two days later, all five young were again present in the nest at 9:30 A.M., but only 4 remained at 11:30 A.M. (Fig. 14). Tracks in the light snow showed that both an adult rabbit, presumably the mother, and the young had been active about the nest during the previous night. They were absent from the nest on the following day and apparently never returned.

Nest No. 3 was found by a farmer in the corner of an apple orchard. It was in a small 6-inch deep bed of straw, about 9 yards from good cover and a frequently travelled highway. On May 5, six days after discovery, the young were still blind. At this time the total weight of all seven young was 14½ oz., the average length of their ears 16.7 mm., and the hind foot 29.1 mm. The eyes of one rabbit was open on May 7, and of two on May 8. At this time the average ear length was 20.7 mm., and the hind foot 35.7 mm. All six young which were in the nest on May 11 were ear-tagged and weighed (total weight, 18.5 oz.). The seventh individual apparently left the nest one day earlier than the remaining six which were gone on May 12, at which time they were known to be at least thirteen days old.

Sex ratio.—Gerstell (1937a) noted the sex of 6,394 live cottontail rabbits shipped into Pennsylvania from Kansas and Missouri for restocking purposes.

He found that, "of the total in question, 3,246 individuals were females, while 3,148 were males, the respective percentages being 50.8% and 49.2%." Trippensee (1936) examined 226 cottontails, of which "... 123 were males, and 93 were females ...", indicating a ratio of 43 per cent females. Allen (1938b) took 383 rabbits by various methods and found that "... 195 were males and 188 were females"; the sex ratio was accordingly 49 per cent females.

Almost all rabbits examined for sex during this study were live-trapped. A few were shot or were picked up dead on the highway. Eight hundred twenty-five rabbits, consisting of 411 females and 414 males, have indicated a sex ratio of 50 per cent females.

A large number of these rabbits were taken on areas closed to hunting during 1939. However, some poaching took place. It is doubtful if the normal sex ratio has been appreciably altered by a higher percentage of males being shot, as might be expected from evidence found by Trautman (Trippensee, 1936) in Ohio, where females were more likely to hole up during cold weather than were males.

Summary on reproduction.—The breeding season of the cottontail has been found to continue from early March to mid-September. This season was determined from a chronological series of measurements on the testes of individual living males, nesting records, autopsies, and by palpating the abdomen of females which were live-trapped.

Individual cottontails in this region frequently have as many as 4 litters in a single season. The average litter size as determined in this study is 5.4. Comparable stages of successive pregnancies were found in 3 females with an average interval of only 29.3 days. Accordingly, cottontails may have fertile oocytes within a day or two after parturition.

The sex ratio among 825 rabbits (411 females and 414 males) handled was 50 per cent females.

WEIGHTS OF COTTONTAILS

Weights were taken of all rabbits live-trapped or found dead on the highway in the vicinity of the experiment station during all the seasons of 1938 and 1939. Many were retaken and weighed frequently during the two years of study, others were weighed only once.

Methods of securing and summarizing weights.—The method of weighing rabbits consisted of putting each individual into a small cloth bag, which was then closed by a purse string at the top. The bag was suspended from a spring scale, and the weight of the animal and the bag read. The weight of the bag was then subtracted from the total, and the weight of the rabbit recorded to the nearest half ounce.

Four hundred seventy-seven individual cottontails were weighed a total of 939 times (Table 7). Average weights have been grouped by ten-day periods. If an individual rabbit was weighed more than once during a given ten-day period, its average weight for that period was determined and included

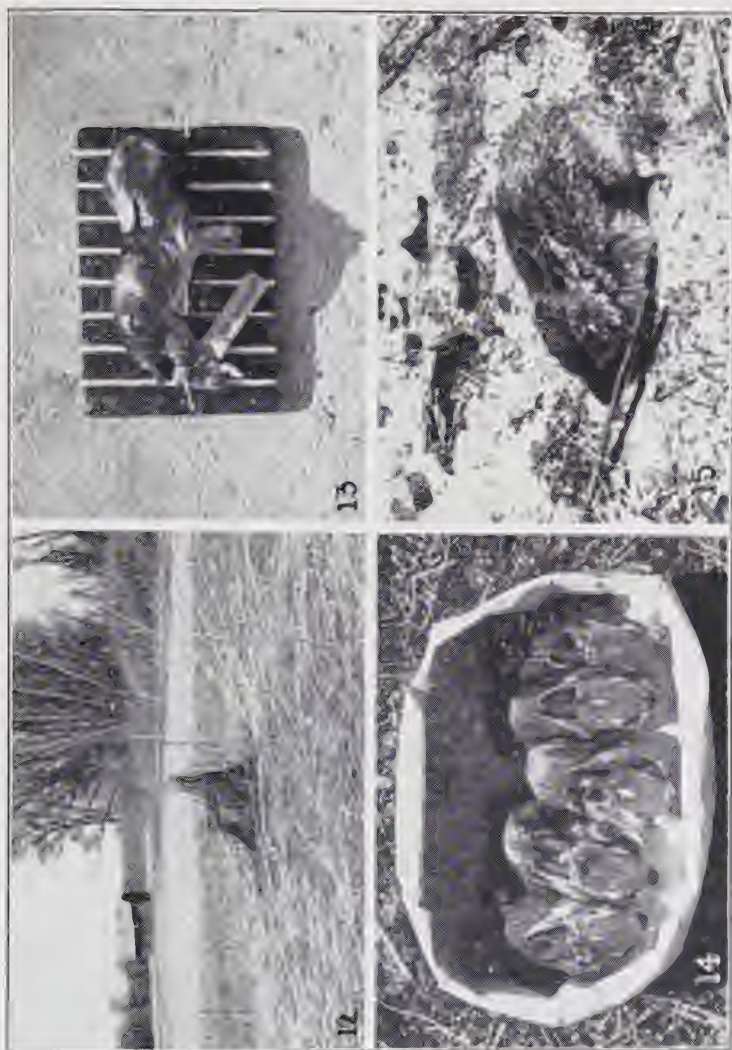


Fig. 12. Nesting site of a cottontail. Nest against base of stump. Fig. 13. A newborn cottontail. Scale: $\frac{1}{2}$ inch between parallel lines. Fig. 14. Young cottontails which will leave nest in a couple of days. April 16, 1939. Fig. 15. Protectively colored juvenile cottontail. Which predator will get him? If he can find the right cover he may live a long time. May 9, 1939.

only as a single datum in calculating the average of the group. The weights of females, males, and juvenile rabbits are given separately. However, it was necessary to combine the data on weights of adults and juveniles after December 10, because some young were as heavy at this time as some known adults. In fact, a few physically mature young may have been unknowingly included in the average weights for adult rabbits during November. The age of most individuals could, however, be ascertained with reasonable certainty until early December. Until this time, the clitori of juvenile females and the testes of juvenile males were usually smaller than the same organs in adult cottontails.

Average weights according to season.—Average weights of cottontail rabbits in this region at the various seasons are: for adult females, 2 lbs. 15.8 ounces during winter, 3 lbs. 3.3 ounces during the breeding season, and 3 lbs. 3.1 ounces during the fall period. Adult males weighed 2 lbs. 13.5 ounces during winter, 2 lbs. 13.2 ounces during the breeding season, and 3 lbs. 2.1 ounces during fall. Average fall weight of juvenile rabbits was 2 lbs. 7.2 ounces for females and 2 lbs. 5.8 ounces for males. Adult females have averaged heavier than males during all periods of the year. This difference in weight between sexes ranged from only 1 ounce during fall to 6.1 ounces during breeding season. Pregnancy was partially responsible for the considerable increase in weight by females during summer. Juvenile females, on an average, were 1.7 ounces heavier than juvenile males during the fall period. According to these figures, females are the larger members of the species at all seasons. The greater weight of females has likewise been noted by Allen (1939), who states that in every group of rabbits sampled, females averaged heavier than the males. This difference in weight varies considerably during the various parts of the year, as will be shown later.

Effects of weather on weights.—Stormy winter weather decreases the weight of cottontail rabbits. Nineteen individual rabbits (8 females and 11 males) which were retaken during more than one of the ten-day periods between January 11 and February 28, show an average decrease of 2.34 ounces in weight. Most of this loss of weight occurred between January 11 and February 10. There were 3.5 inches of snow on the ground on January 18, and a snow-storm accompanied by a stiff northwest wind occurred on January 22. By January 27, 10 inches of loose snow were on the ground. Rabbits were moving very little during this inclement weather. Several cottontails were found occupying burrows, and 2 or 3 were caught while they were sitting in snow-covered forms. This indicated that fresh snow covering the food supply was keeping rabbits under cover. Accordingly, their loss of weight was probably due to lack of proper food. The 8 females lost an average of 3.56 ounces each, while the 11 males lost an average of only 1.46 ounces each. Females lost 3.2 times as much weight as did males. This indicates that males may be less affected by winter weather than are females. However, the data are too inadequate to allow any definite conclusion. A decrease in weight in winter by cottontails was also noted by Allen (1939), who found that a group of rabbits taken in December were 1.7 ounces heavier than another group live-trapped during March. The greater loss of weight in my rabbits is not significant.

The apparent rise in average weight by females between January 20 and January 31, is not significant, because this average is based on only three individuals (Table 7). Two of the females included in the average weight for this period had each lost an average of 4.25 ounces during this period, but the third, a newly taken individual, was large enough to raise the average.

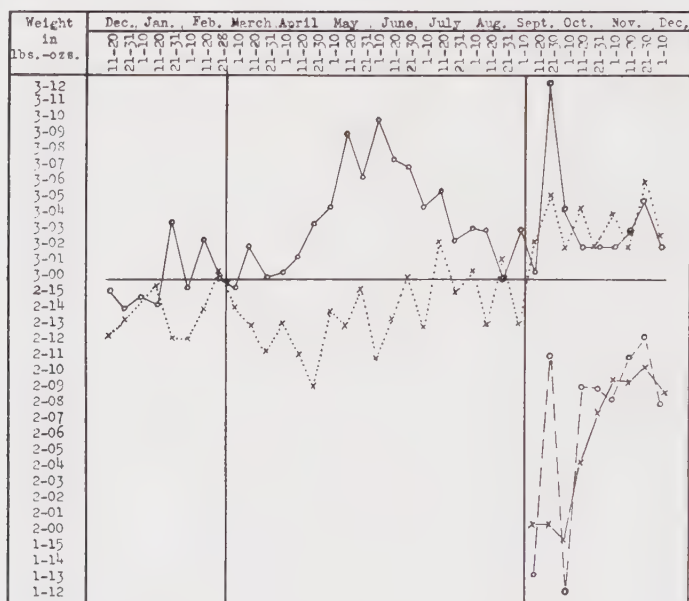
Fluctuations in weight of pregnant females.—Individual females often varied considerably in weight from day to day during pregnancy. As an example, female No. 449 weighed 3 lbs. 8 oz. when she was first trapped on July 11. At that time, she was carrying uterine swellings about the size of a hazelnut. During the ensuing 8 days, she was retrapped daily and gradually lost 4 ounces of weight. When she was taken on July 29th, she weighed 3 lbs. 4 oz. and contained embryonic swellings about the size of a walnut. During the next 6 days, she was retrapped 6 times and regained 4 ounces of weight. This gain in weight occurred at the time during which the embryonic swellings increased from the size of a walnut to a size indicative of embryos approaching full term. In this case, it seems possible that the rabbit may have lost some of its weight because of the constant retrapping, but that the weight of the rapidly growing embryos, the increase in uterine tissues, and the increase in fluids finally compensated for the earlier loss.

The average weight of females gradually increased from 2 lbs. 15.5 ounces in late March to 3 lbs. 9.5 ounces in early June. The average weight gradually decreased during July and August. The increased average weight of females during the breeding season is probably due both to an increase in amount of flesh and their gravid condition.

Except for minor fluctuations, the average weight of adult females changed very little during the fall months.

Seasonal fluctuations in the weight of males.—The weight of adult males does not vary as greatly during the year as does that of females. Average weight of males increased during December and until it reached 2 lbs. 15 oz. in the middle of January. Three and one-half ounces of weight were then lost on the average during the last part of January, because of the inclement weather previously discussed. Males made a slight average gain in weight during the last 20 days of February. At the start of the breeding season (March 1), males were in the best condition (3 lbs.) attained during the winter period. From this time on, however, the average weight of males decreased rapidly until in late April it was only 2 lbs. 8.5 oz. This loss was probably due to an increase in activity during the breeding season. Their average individual range (Haugen, in press) was very large (perhaps 100 acres) at this time of the year. At about the time green vegetation became available (late April) males began to regain some of the weight they lost during the first two months of the breeding season. They continued slowly to gain weight until the middle of September, at which time they averaged 3 lbs. 2 oz. (Graph 2). A sudden rise in average weight (increase to 3 lbs. 5 oz.) during September coincides with the ending of the breeding season.

Increase in weight by juvenile cottontails.—Individual weights of juvenile



Graph 2. Seasonal variations in weights of cottontail rabbits. Key: o——o adult females; ×....× adult males; o——o juvenile females; ×——× juvenile males.

rabbits vary widely during the fall period. This is expected because of the large age differences in litters born during the various parts of the breeding season (March to September). Weights of 62 juvenile rabbits taken between September 11 and 20 are dispersed evenly between 11 ounces, and 2 lbs. 13 oz. The amount of deviation from the mean steadily decreases as the fall period progresses. The range of variation of the weights of juvenile rabbits was reduced to 10.5 ounces (2 lbs. 3.5 oz. to 2 lbs. 14 oz.) by the first of December. Average weights of the juveniles are unreliable because of the wide variability of individual weights. However, there is a rapid increase in average weight from September through November (Table 7).

Summary on cottontail weights.—From the evidence presented, it is apparent that weather, season, pregnancy, age and sex have a considerable effect on the weight of the cottontail. Adult females increase considerably in weight during the breeding season, reaching their maximum average weight during early June. The average weight of males, however, decreased considerably during March and April, then slowly increased during the last two-thirds of the breeding season. A further gain in weight by males was noted as the breeding season came to a close. Weights of adult females and males both averaged about 3 lbs. 2.5 oz. during October, November, and early December, but at other seasons, females were always the heavier. A further rise in weight by adult rabbits occurred during the middle of December. Some juvenile rabbits,

however, were as heavy as many adults at this season, and it is therefore necessary to combine weights of all individuals of the same sex after December 11. Inclement weather during January and early February 1939, resulted in an average decrease of 2.34 ounces of weight.

TABLE 7.—Seasonal Weights of Cottontail Rabbits.

		Adult				Juvenile			
		Female		Male		Female		Male	
		Number weighed	Mean weight	Number weighed	Mean weight	Number weighed	Mean weight	Number weighed	Mean weight
Dec.	11-20	8	2-15.0*	16	2-12.0*				
	21-31	5	2-13.5	12	2-13				
Jan.	1-10	5	2-14.5	0					
	11-20	7	2-14	6	2-15				
Feb.	21-31	3	2-02.5	4	2-11.5				
	1-10	6	2-14	13	2-11.5				
	11-20	8	3-02.5	13	2-13.5				
	21-28	4	2-15.5	8	3-00.5				
Winter		46	2-15.8	72	2-13.5				
March	1-10	10	2-15	18	2-13.5				
	11-20	13	3-01	15	2-12.5				
	21-31	16	2-15.5	18	2-11				
April	1-10	15	3-00	17	2-12.5				
	11-20	25	3-01	21	2-10.5				
	21-30	9	3-03	9	2-08.5				
May	1-10	12	3-04	7	2-13.5				
	11-20	11	3-08.5	14	2-12.5				
	21-31	14	3-06	5	2-15				
June	1-10	5	0-09.5	2	2-10.5				
	11-20	13	3-07	7	2-13				
	21-30	11	3-06.5	7	2-15.5				
July	1-10	11	3-04	2	2-12.5				
	11-20	13	3-05	4	3-02				
	21-31	23	3-02	13	2-14.5				
August	1-10	12	3-02.5	5	3-00				
	11-20	7	3-02.5	3	2-12.5				
	21-31	9	3-15.5	7	3-00.5				
Sept.	1-10	13	3-02.5	10	2-12.5				
	Breeding Season	—	—	—	—				
		242	3-03.3	184	2-13.2				
Sept.	11-20	3	3-00	4	3-02	31	1-12.5	32	2-00
	21-30	1	3-12	1	3-05	3	2-10.5	9	2-00
Oct.	1-10	5	3-04	2	3-01.5	4	1-11.5	8	1-15
	11-20	3	3-01.5	2	3-04	12	2-08.5	11	2-05
Nov.	21-31	9	3-01.5	10	3-01.5	21	2-08.5	23	2-07
	1-10	7	3-01.5	3	3-03.5	33	2-08	35	2-09
	11-20	7	3-02.5	4	3-01.5	36	2-10.5	32	2-09
	21-30	2	3-04.5	2	3-05.5	18	2-12	12	2-10
Dec.	1-10	1	3-01	2	3-02	3	2-07.5	4	2-08
Fall		38	3-03.1	30	3-02.1	161	2-07.5	166	2-05.8

* Weight given in pounds-ounces.

PARASITES OF THE COTTONTAIL RABBIT

Degree of infestation by ectoparasites has been carefully observed on most of the 825 individual cottontails captured during 1938 and 1939. Several of these individual rabbits were reexamined repeatedly during one or more seasons during the two years. At each examination, the degree of infestation by fleas, ticks, and mites was recorded as "light," "moderate," or "heavy." The presence of 5 or 6 individuals of a parasite was called a moderate infestation, while a greater number was considered indicative of heavy infestation. Dead rabbits were sent to the Pathology Laboratory of the Michigan Department of Conservation at East Lansing to be examined for endoparasitic infection.

ECTOPARASITES

Fleas.—Rabbits have usually been infested with a moderate number of fleas during all months of the year. Dr. J. C. Bequaert of Harvard University identified a single specimen as *Cediopsylla simplex* Baker, the common species on cottontail rabbits. The degree of infestation on a single individual cottontail often varied from day to day. This variation is believed to have been in part caused by errors in observing the degree of parasitism. Rabbits which were recorded as free from infestation may have harbored a few hidden fleas. Most of the fleas were usually congregated on the head region of the rabbit.

The only observed ill effect suffered by rabbits from parasitism by fleas was a severe irritation of the hairless inner fold on the anterior edge of the ear. At times during winter, 8 to 10 more fleas occupied this hairless crease. Such extreme cases were usually accompanied by signs of bleeding on the infested area.

Ticks.—Ticks have been found in moderate to small numbers during all months of the year except December, January and February, when they were apparently absent. The only tick found on the cottontail during these 3 winter months was observed on January 17, 1939. Dr. J. C. Bequaert of Harvard University has identified ticks collected from the cottontails as *Haemaphysalis leporis-palustris* (Packard). During March, frequency of infestation by ticks became increasingly greater. A moderate infestation continued until early November, after which their numbers decreased rapidly.

The common point of infestation by ticks was at the base of the ears, and in the short hair about the eyes. Occasionally, they were found in the hairless inner surface of the anterior fold of the ear, as were the fleas. No apparent ill effect from tick infestation has been observed.

Mites.—Mites were found on 6 individual rabbits, and on one litter of young. It is believed, however, that many cases of mite infestation escaped detection. They are so extremely small that they were seen only with a very close examination. In fact, mites escaped detection entirely during 1938. Dr. H. E. Ewing of the U. S. Bureau of Entomology has kindly identified the 3 genera of mites which were found on the cottontails.

Articholaelops glasgowi (Ewing) a mite common on many species of

North American Mammals was abundant on some nestling rabbits found on April 12, 1939. No other records were secured.

Cheyletiella sp., a predaceous mite that feeds on true ectoparasites, was secured from adult cottontails in October, 1939. These mites were found at the base of the head just posterior to and between the ears.

Euhaemagamasus sp., a true parasitic mite, was taken from a cottontail on April 1, 1939. Only a single specimen of this species of mite was collected.

Mange-like condition of skin.—Nine individual rabbits were found with various degrees of flakiness of the skin, but no scab mites were observed. The most extreme mange-like condition was observed on an individual autopsied on April 20, 1939 (Fig. 16). This adult male rabbit was exceedingly emaciated, without hair on the posterior ventral side, and only sparsely furred on the rest of the body. Scrapings were taken from the skin of this animal, and the scaly looking debris examined under a microscope, but no scab mites were found.

Warble fly larvae.—The larvae of two species of warble flies live in cottontails in this area. These species were identified by Dr. Bequaert as *Cuterebra cuniculi* Clark, and *Cuterebra buccata* Fibricius. Parasitism with these pests first became evident during the middle of November. As many as 8 larvae have been observed on a single rabbit at one time. The ventral side of the body is most frequently parasitized, especially the throat and chest region (Fig. 17). Occasionally, larvae were found in the inguinal region (Fig. 18).

One adult fly of *Cuterebra buccata* was incubated from a larva dropped from the scrotum of a rabbit on September 4, 1938. The larva was allowed to burrow into the ground by its own effort (2 inches below surface). On the following day it was transferred into a tin can containing sandy soil. The pupa was buried two inches below the surface of the soil in the can. The can with lid attached, and with top and bottom punched full of nail holes, was then buried flush with the surface of the ground. The nail holes allowed moisture to pass through the can. This improvised incubator was examined for signs of



Fig. 16. Cottontail with a mange-like condition of the skin. April 20, 1939. Fig. 17. Five warble fly larvae on throat of cottontail. Photo by D. L. Allen. Fig. 18. Warble fly larva in scrotum of male cottontail. August 17, 1939.

emergence on several occasions in the early summer of 1939. On July 2, 1939, the fly was found emerged, but dead and partly destroyed by small ants. According to the schedule of examinations of the incubator, this fly emerged on about June 28, 1939. The larva therefore emerged after 297 days of pupation.

Three specimens of *Cuterebra cuniculi* were incubated. On July 26 and 27, 1939, four warble larvae from cottontails were put into two containers and covered with about 2½ inches of damp sand. Both containers were then left in a cool, damp basement room and slightly watered on a few occasions. On September 15, 1939, the first fly was found sitting on the underside of the cheese cloth which enclosed the top of the can. According to schedule of examinations, this specimen emerged after 61 to 63 days of pupation. Two of the remaining three pupae were found emerged on June 8, 1940, 316 or 317 days after leaving the rabbit. One of the individuals (alive) had apparently emerged on this date, the other was dead and probably emerged a few days earlier. Further records were not kept on the fourth pupa.

ENDOPARASITES

Twenty-one cottontails killed near the experiment station mainly during December, January and February were examined for endoparasites and pathogenic conditions.

The per cent of individual cottontails infected by endoparasites was found to be as follows:

	Individuals parasitized	Per cent of individuals parasitized
Sporozoa <i>Eimeria</i> sp.	11	52%
Trematoda <i>Hasstilesia tricolor</i>	7	33%
Cestoda <i>Taenia pisiformis</i>	10	48%
<i>Cittotaenia pectinata</i>	14	67%
Nematoda <i>Trichostrongylus</i> sp.	5	24%

Coccidiosis.—Eleven rabbits (52%) were infected with two species of *Eimeria*. Infections were never found serious in either adult or juvenile wild rabbits, but one juvenile captive cottontail died from a severe case of coccidiosis during the summer of 1939. This juvenile had been held in captivity for 2 months. A necropsy revealed a distended, necrotic condition of the caecum which was 2 inches long and three-fourths inches in diameter. The entire cavity of the caecum was filled with a "cheesy" looking liquid swarming with coccidia oöcysts.

Yeast.—An extraordinarily heavy concentration of yeast was found in the small intestines of a juvenile cottonwood which died in captivity during the summer of 1939. A case of diarrhea accompanied the condition.

Trematoda.—*Hasstilesia tricolor*, a fluke, was found in 7 rabbits (33%). Rabbits secured from damp lowland habitats during winter were found to have the most severe infections. The intermediate host of this species probably occurs more frequently in those habitats.

Cestoda.—Larvae of the dog tapeworm, *Taenia pisiformis*, were recovered in 10 cottontails (48%). The number of these cysticerci present in a single cottontail has varied from 1 up to 50. The small bladder larvae were found throughout the body cavity.

The rabbit tapeworm, *Cittotaenia pectinata*, has occurred in 14 of the rabbits (67%) autopsied. In no instance were more than four of these tapeworms present at one time.

Nematoda.—Five cases (24%) of infection with *Trichostrongylus* sp. were found. The degree of parasitism was small in each case.

PAPILLOMAS

Forty cases of papillomas, or "horns," were found among rabbits live-trapped. Affected rabbits were found only between September 1 and December 13, and the abnormality was limited almost entirely to juvenile or sub adult rabbits. Only 2 of the 40 cases were found on rabbits which were definitely 1 year or more old. The flesh colored swellings most frequently occurred on the feet (Fig. 19), but were also found on the nose, eyelids, lips, ear and back. Rarely, have the swellings reached the size of an inch in diameter.

Tumors evidently disappear from the affected cottontails during winter. Three rabbits which showed tumors in the fall of 1938 were without the gruesome looking warts when recaptured in the summer of 1939.

DISCUSSION OF EFFECTS OF PARASITISM

One case of mortality among cottontails handled during the investigation has been attributed to parasitism. In this case, death resulted from a very severe case of coccidiosis suffered by a juvenile captive rabbit. A second juvenile

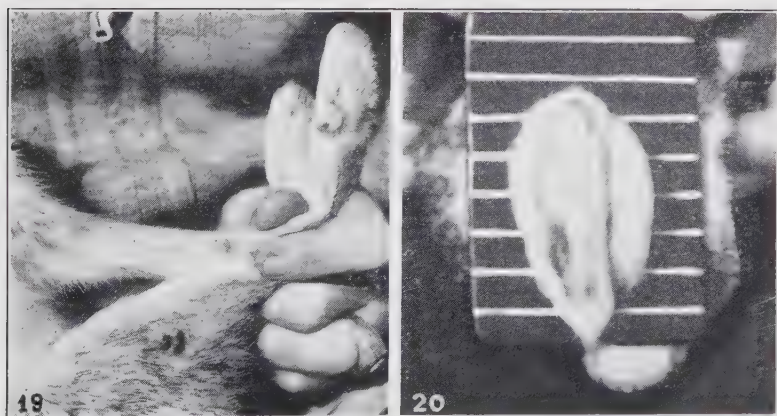


Fig. 19. Papillomas or "horns" on the legs of a cottontail. Photo by D. L. Allen. Fig. 20. Size of cottontail testes on April 1, 1939. Note degenerate left testis. Warble fly larvae parasitized scrotum in 1938. Scale: $\frac{1}{2}$ inch between lines.

rabbit which died unexpectedly in captivity harbored an abnormal concentration of yeast in its intestines and showed signs of diarrhea. It is not known for certain if death resulted from the overabundance of yeast.

A moderate infestation with fleas, ticks, mites, or a moderate infection with trematodes, cestodes and nematodes did not seem to have any apparent influence on the well-being of cottontails. In fact, heavily parasitized rabbits were frequently very fat.

The presence of a mange-like condition in rabbits has not reached a sufficiently large incidence of occurrence to be of any importance. Perhaps some of the 9 cases observed were contracted from the cloth bag which had been used to weigh both rabbits and squirrels. Many of the squirrels which were placed in the bag exhibited severe cases of scab.

Warbles have in three cases caused an abnormal condition of one testis of male rabbits. After the parasitic larva had left its position in the scrotum of the rabbit, it was found that the afflicted testis was very small and degenerate. As far as could be determined, the opposite testis was normal. A year later, it was found that the damaged testis of one rabbit had recovered. The afflicted testis of a second male still remained degenerate the following breeding season (Fig. 20). It seems possible from this evidence that warble fly larvae could in rare instances cause sterility.

The psychic effect on a hunter of the presence of heavy infestations of parasites on rabbits is of importance. Probably, many a rabbit has been discarded because of its unsightly appearance due to the presence of warbles, papillomas, or cysticerci. Warbles ("grubs") disappear from cottontails suddenly in early November.

Accordingly, if the opening of the hunting season on cottontails were delayed until November 15, the waste of meat resulting from the discarding of rabbits with unsightly warbles ("grubs") could be eliminated.

SUMMARY ON PARASITES

Two species of warble fly larvae commonly parasitize the cottontails in this region from July to mid-November. The presence of warble larvae in the scrotum of rabbits caused temporary degeneration of the testis in one rabbit, and permanent degeneration in the testis of a second rabbit.

A flaky, mange-like condition of the skin has been found on nine cottontails during the two years of study.

Fleas and ticks were found in moderate numbers on the cottontails in this region. Fleas were present at all seasons, but ticks were not observed during winter, except on one occasion.

Two species of parasitic and one species of predaceous mites were found during the summer and fall.

The most severe cases of infection with a fluke, *Hasstilesia tricolor*, were found in rabbits taken near bogs and from the lowland.

Two species of tape worms and one of round worms were found in several of the cottontails examined.

The presence of a moderate number of one or more of species of parasites found in the cottontails did not seem to effect the well-being of the individuals to any great extent. In fact, many of the parasitized rabbits were fat.

LONGEVITY

Of 73 adult cottontails (34 females, 41 males) marked during the 1938 breeding season, 21 (6 females, 13 males) were retaken during some part of the 1939 breeding season. These adult rabbits must have been a year or more old when marked in 1938. Accordingly, a minimum of 25 per cent of the 1938 adult population lived to an age of approximately 21 or more months. It is likely that some of the marked rabbits emigrated from the areas studied, and were therefore not retaken. In that event, the per cent of rabbits which reached the age of 21 or more months was larger than indicated. This high per cent (25) of survival to breed 2 or more seasons may be due to the fact that the areas were closed to legal shooting during 1938. However, some poaching did occur. Allen (1939) states, "Of 70 rabbits marked . . . during the first 3 months of 1936, only 12 are known to have lived to the following November." Accordingly, adult cottontails on the areas studied by me were surviving longer than was indicated by Allen's farmland studies. Seven of 29 (24%) cottontails (*Sylvilagus audubonii audubonii*) studied by Ingles (1941) were known to have lived longer than one year.

MORTALITY

PREDATION

New York weasel (Mustela frenata noveboracensis).—Eighteen cottontails were attacked and killed by weasels, which entered through the inch-mesh wire covering on some of the traps. Even traps covered with half-inch hardware cloth did not adequately protect rabbits from weasel attacks. Weasels also entered a few traps through a one and one-fourth-inch hole in the metal door, or made excavations under the wire floor of the trap and attacked the soles of the rabbit's feet. On a few occasions, the flesh was stripped from the toes of the captive rabbit, leaving the bare bones exposed. Such injury probably resulted in ultimate death. One weasel was observed in the act of killing a juvenile rabbit in the wild. Hickie (1940) states that "In making the rounds of its range, the weasel seems to visit each of the holes with which it is familiar." A rabbit cornered by a weasel in a burrow can usually escape (p. 237). Evidence indicates, however, that the weasel is responsible for more cottontail mortality than is any other predator on the area.

Dogs.—During 1938 and 1939 dogs were repeatedly seen in pursuit or possession of cottontails. Two rabbits were definitely known to have been killed by "self-hunting" dogs, and four other dead cottontails were found in the possession of dogs. On three occasions, dogs were found attempting to excavate an animal (probably a rabbit) from a burrow. It was not unusual to find tracks

of dogs in the study areas. A small collie and a large mongrel hound were repeatedly found hunting rabbits on an area three miles in diameter.

Domestic cat.—During 1939, two cottontails were found killed by cats. One of these rabbits contained 4 embryos. Only about 4 individual cats were taken in the live-traps during 1938 and 1939. These were ear-tagged and released in an attempt to determine their range of activity. One adult male cat which had been deserted at a farm which was abandoned was trapped 3.2 miles from its home. It was later discovered back at the abandoned farm home. Two or three other cats on the area have evidently existed in the feral state for 2 or more years. My observations support the statement by Hickie (1940) that stray dogs and cats “. . . take far too large a toll of wildlife while offering nothing in return.”

Opossum (Didelphis virginiana).—Only one cottontail was found dead from what appeared to be predation by opossum. The remains of this adult rabbit were found partly pulled into the base of a standing hollow tree. Only a portion of the hind quarters were eaten. Blood stained spots on the inside of the skin of the head and neck region indicated that the rabbit was bitten while still alive.

Red fox (Vulpes fulva).—Information on the interrelationship of fox and cottontail in the areas studied is lacking. Tracks of foxes were found on a few occasions during 1938 and 1939.

Coyote (Canis latrans).—At least one coyote was present in the region during 1939. No signs of predation were found.

Badger (Taxidea taxus).—A badger den was located on one of the management areas, and trails of this species were frequently observed, but at no time was evidence found which indicated predation on rabbits by badgers.

Raccoon (Procyon lotor).—Raccoon are common on the areas. No signs of predation on cottontails were found.

Hawks.—Broad-wing (*Buteo platypterus*), red-tail (*Buteo borealis*), and marsh hawks (*Circus hudsonius*) prey on the cottontail in this area. One nest of each species was located. In each case, there was an apparent scarcity of rabbits in the immediate vicinity of the nest. Fur of juvenile cottontails was abundant about the broad-wing hawk's nest. Size of the hind feet of all rabbit remains taken from the marsh hawk nest indicated that nothing larger than an immature rabbit was eaten. Red-tail hawks have been found feeding on the remains of adult cottontails. Hickie (1940) states that the “big hawks” lose importance because “. . . mostly young, instead of adult rabbits appear in their diet. . . .” It should be remembered, however, that a dead young rabbit can never become a live adult.

Owls.—Fresh cottontail remains were found on several occasions in the nests of both Barred (*Strix varia*) and Great Horned (*Bubo virginianus*) owls. Juvenile as well as adult rabbits were represented. Owls were found nesting only in the large timber on the lowland. The greatest predation pressure by these two species was probably exerted on the cottontails occupying the lowland.

Crow (Corvus b. brachyrhynchus).—One freshly-killed juvenile rabbit was taken from a crow. The hind foot of the rabbit was 40 mm. in length, which indicates that it had either been taken from, or had only recently left, the nest.

Black Snake (Elaphe obsoleta obsoleta).—Two juvenile cottontails were recovered from a 5½-foot black snake collected on the area by R. D. Montgomery. One of the young taken from the stomach of the snake weighed 78 grams and its hind foot measured 42 mm. The size of this rabbit indicates that it was about 15-16 days old, at about which age cottontails leave the nest.

MORTALITY FROM EXPOSURE IN TRAPS

Only 7 rabbits died during the study from exposure in traps. Six of these rabbits were overcome by heat, and one died in a trap during severe winter weather. A rabbit can evidently not endure direct exposure to hot summer sunlight for more than a few hours. As a precautionary measure during summer, traps were placed in shade whenever possible. No rabbit should be allowed to remain in a trap exposed to direct summer sunshine later than 9 A.M. The single mortality from exposure in a trap during cold weather occurred on a night with a fresh snowfall and a minimum temperature of 10 degrees Fahrenheit.

HIGHWAY MORTALITY

During 1938 and 1939, 31 cottontails were found dead on Highway M89, and the side roads between Allegan and the experiment station. This number included 12 females, 13 males, and 6 of unknown sex. None of the females examined was pregnant.

During the latter years, numerous papers have appeared listing the numbers of rabbits killed by highway traffic. I do not believe the effect of such mortality is as serious as is often suggested. Automobiles merely kill the rabbits and leave the resulting carrion for other species to devour. Predators which are attracted to the highways by the carrion will have less necessity to kill their own prey. Undoubtedly, a few predators so attracted will themselves become traffic victims.

INJURIES

Seventy-six individual rabbits from a total of 2,113 captures (includes recaptures) have injured themselves while captive in traps. These injuries were as follows: skinned forehead and nose, 68; broken toes, 7; broken leg, 1; and one struck across the neck by the falling trap door.

The skin of ten individual rabbits was torn while handling. The skin of juvenile rabbits is very susceptible to tearing. However, tears in the skin were frequently mended by bringing the torn edges back together and then matting chewing gum into the fur along the tear. The young have often survived severe tears in the skin.

None of the rabbits trapped has shown signs of serious injury received in nature. However, their ears and back frequently showed scars which were evidently signs of combat.

PREDATION ON COTTONTAILS IN BURROWS

Usually, when a shortage of rabbits becomes apparent, the public casts the blame on predation. Often it is claimed that opossums, weasels and skunks raid burrows and eat the cornered rabbits. Seton (1929) tells of the destruction by skunks and weasels of rabbits in burrows.

EXPERIMENTAL EVIDENCE ON PREDATION IN BURROWS

Ten individual experiments on predation by skunks, opossums, and weasels on rabbits occupying burrows were performed. Facilities for the experiment consisted of a specially constructed burrow with an attached lightproof observation pit, and a two-compartment pen above ground. A drop door regulated by a string was used to control the movement of the predator from one compartment of the pen to the other. One end of the pen was connected to a wire-lined burrow (about 6" diameter) which led downward at a grade of about 25 degrees. At a point 6 feet from the pen and 3 feet below the surface of the ground, the burrow reached the side of the observation pit, turned, and continued parallel along two sides of the pit. A piece of glass from an old car windshield was used to form the side of the burrow which was open to view from the observation pit. The burrow had only one exit. The pit was provided with a light-proof lid so that the observer could sit unseen as he watched the animals with a flashlight covered with red cellophane. On a few occasions, the animals assumed a cautious attitude towards the light; at other times, they ignored it.

Experiments with a skunk (Mephitis mephitis nigra).—Four separate trials were made to see if a hungry skunk would kill a rabbit confined in the experimental burrow. An adult skunk which had been in captivity for about 3 months, and wild adult cottontails were used in the experiments. The skunk, which had been starved for 4 or 5 days prior to the experiment, was introduced into the burrow which contained an adult rabbit. From the observation pit, it was observed that the skunk pursued the rabbit downward. At the end of the burrow, the rabbit quickly turned and met the skunk head on. It quickly forced its way past the skunk and dashed out of the burrow. The skunk remained with a mouthful of rabbit hair. Two additional experiments gave similar results. On a fourth trial, the rabbit stayed at the end of the burrow facing the skunk, but seemed to be sitting or lying on its rump, kicking viciously with both hind feet. The skunk was thus effectively warded off. Shortly after the light was flashed on, the skunk backed away about a foot and remained motionless. The animals were left in this position. Next day the rabbit was found sitting in the pen; the skunk was asleep in the hole.

Experiment with an opossum.—An adult wild opossum which had been starved for 10 days was introduced into the predation burrow containing a rabbit. The rabbit retreated to the end of the burrow as the opossum approached downward. The opossum had to be prodded downward into the hole. As it came close to the rabbit, it seemed to bare its teeth in a defensive snarl and shrank back slightly at each movement of the rabbit, which seemed unalarmed. After about half an hour of observation with no action, the animals

were left to themselves. On the following day, the opossum was found curled up asleep in his pen above ground.. The partly eaten rabbit lay at his side. It is possible that the rabbit escaped from the burrow and into the pen before it was killed, as there was no fresh blood in the burrow.

Experiments with a New York weasel.—Four different weasels were used in five experiments on predation of rabbits in the experimental burrow. Each of these weasels was live-trapped and was denied food on the day of the experiment.

An adult male weasel was allowed to enter the experimental burrow which contained an adult female cottontail. At the time the weasel entered, the rabbit sat facing outward at a point 3 feet from the end of the burrow. The weasel came directly to the rabbit, which remained motionless. As the weasel's nose touched the fur of the rabbit, it seemed to hesitate momentarily, then charged the rabbit, trying to secure a hold at the base of the skull. The rabbit quickly backed down the burrow a foot or two, then dashed forward, forced its way past the weasel, and ran from the burrow. The weasel gave up pursuit at the mouth of the burrow. Apparently, the rabbit was unharmed.

During an additional experiment with other individuals, the rabbit sat facing downward in the burrow when the weasel made his initial attack, attempting to secure a hold at the nape of the neck. This rabbit ran to the end of the burrow where it sat with its nose in the far corner. As the weasel rushed in to secure a hold on the neck, the rabbit quickly turned by rotating its head to a direction away from the weasel, and escaped unharmed from the burrow.

In only one of five experiments did a weasel follow the rabbit into the pen and continue the attack. This weasel succeeded in killing the rabbit after about 2 minutes of intermittent attack. Its killing technique consisted of striking the rabbit at the base of the neck, inflicting one or two bites, and then retreating. After about one and one-half minutes of repeated attacks, the rabbit became increasingly weak. As soon as the rabbit became too weak to dash wildly about the pen, the weasel struck again and hung on, biting viciously at the base of the skull until the rabbit was dead. During one of the early attacks, the rabbit was successful in dealing the weasel a severe blow by means of its hind legs, but this blow did not discourage the weasel. The chief aim of the rabbit seemed to be to find some avenue of escape.

In each of the five experiments with weasels and rabbits, the rabbit emerged unharmed from the burrow.

DISCUSSION OF PREDATION IN EXPERIMENTAL BURROW

Experiments on the vulnerability of cottontails occupying an artificial burrow have shown that their defense from the attacker has consisted mainly in flight. In this situation, however, the only means of flight for the rabbit was to charge the enemy head on and force its way past. This the rabbits did successively in 9 of the ten experiments. On the tenth experiment a cottontail successfully ward off a skunk by sitting at the end of the burrow and thrash-

ing the skunk with its powerful hind legs. Seton (1929) relates how one Rev. Griggs H. Thompson, in Missouri, observed a cottontail leaping over the body of a skunk, striking it with its hind feet. He says the skunk had been dead only a few minutes. In defense of their young, cottontails have been found to similarly attack a cat (Ingersoll, 1907) and a snake (Kennicott, 1857). Although rabbits may sometimes be killed in burrows in the wild, the evidence from my experiments indicates that rabbits are often able to escape or to defend themselves against attack.

SUMMARY ON MORTALITY OF COTTONTAILS

Weasels, stray dogs, and feral cats, in the order listed, are important enemies of cottontails in the area. Only one case of rabbit mortality has been attributed to the opossum. Such predators as fox, badger, coyote and raccoon occurred on the area, but no evidence was found to indicate their relationship to the cottontail.

The avian foes of the rabbit consist of hawks (Red-tail, Marsh, and Broad-wing), owls (Great Horned and Barred), and crows.

No rabbits have died in live-traps from injury suffered while struggling to escape, but 6 individuals succumbed from exposure to summer sunlight, and 1 from exposure to severe winter weather.

Experiments on the vulnerability of cottontails which occupy burrows has shown that they are capable of escaping from opossums, skunks, and weasels which attempt to prey on them in burrows.

The most serious predation in the region resulted from the activity of hawks and weasels.

INDIVIDUAL RANGE OF COTTONTAILS

Home range requirements of adult female cottontails on sandy upland areas were 22.5 acres during the breeding-season; during fall, slightly over 15 acres; and during winter, 14 acres (Haugen, in press). Adult males roamed over an area probably 100 acres or more. During late summer, juvenile rabbits occupied an average of 9.3 acres. This area increased with the development of the young until fall at which time the juvenile females occupied 14.6 acres and the males 13.5 acres.

In southwestern Michigan, breeding female cottontails occupied home ranges which were rarely trespassed upon by other breeding females (Haugen, in press). Adult males, however, seemed to roam over large areas in search of mates, which they apparently soon forsook to search for others. Home ranges of males accordingly overlapped indiscriminately.

Cottontail populations.—On an average, the breeding population of cottontails on the sandy upland (1938 and 1939) consisted of about one rabbit per 17 acres (Haugen, unpublished manuscript). During fall, the population increased to one rabbit per 10 acres. The extremes in cottontail populations on the six 160-acre study areas consisted of a minimum of one rabbit per 32 acres during spring, and a maximum of one rabbit per 7 acres during fall.

EFFECT OF COVER ON POPULATION DENSITY

A relationship has been found to exist between the density of the cottontail population and the type of cover available. This relationship has been demonstrated by live-trapping rabbits at stations spaced at 110-yard intervals in a pattern, with a relationship similar as have the center points of each of 49 contiguous squares on a checkerboard. Each square represents an area of 2.5 acres with a trap station at its center (Haugen, in press). The cover on such a trap square, extending half the distance to the nearest surrounding trap stations, will statistically have the greatest influence on the number of rabbits captured at the given station. It is recognized, however, that the number of rabbits caught at any trap station will be influenced in part by the cover on adjacent trap squares. By comparing the catch of cottontails at various trap stations, with the cover densities of the respective trap squares, it is possible to evaluate the influence of cover on the population of rabbits.

The densities of the forest canopy on 293 trap squares on the management areas have been classified as follows: below 12.5 per cent, 25, 50, 75, and above 87.5 per cent dense (Table 8). As an example, I have considered that a canopy which is 50 per cent dense will on the average shut out from 37.5 to 62.5 per cent of the sunlight. The classification was made from the appearance of the cover on an aerial photograph, aided by my knowledge of the area.

Effect of cover on catch during breeding season and fall.—Trapping results during the breeding season and fall show that in trap plots with less than 12.5 per cent of forest canopy, a catch equal to 4.65 per cent of the trap nights (one trap set one night called a trap night) was secured; under a 25 per cent canopy, there was a 3.86 per cent catch; under a 50 per cent canopy, 3.46 per cent catch; under a 75 per cent canopy, 2.38 per cent catch; and under a canopy

TABLE 8.—Relationship of the Density of the Forest Canopy to the Catch of Rabbits During the Breeding Season, Fall and Winter.

	Completeness of forest canopy	Number trap squares	Number rabbits	Number trap nights	Per cent trap nights filled
During breeding season and fall:					
below	12.5%	32	208*	4,473	4.65
	25.	47	241	6,251	3.86
	50.	57	252	7,292	3.46
	75.	64	186	7,802	2.38
above	87.5%	93	263	11,304	2.32
During winter:					
below	12.5%	32	3	384	0.78
	25.	47	8	459	1.74
	50.	57	4	362	1.10
	75.	64	18	752	2.39
above	87.5%	93	53	1,469	3.63

* Sum of all rabbits taken on given trap squares. Each individual rabbit counted once for each trapping period in which it was captured on the trap square.

denser than 87.5 per cent a catch equal to only 2.32 per cent of the trap nights was taken (Table 8). It is evident that as the density of the forest canopy increased, the per cent of catch per trap night decreased. In other words, the size of the catch varied inversely with the density of the forest canopy.

Roughly, the number or density of shrubs varied on the trap squares inversely with the density of the forest canopy. The abundance of shrubs is dependent upon the amount of sunshine which reaches the ground. Trapping records, accordingly, show that the population density of rabbits on an average varies directly with the amount of shrubs present. This information can be used in managing an area for cottontails. Thus, by opening the forest canopy to encourage growth of shrubs, it can be expected that an increase in the population of cottontails will result. In support of this evidence, Morton and Sedam (1938) in Pennsylvania have found that cottontail populations increased in areas where release cutting was practiced. Allen (1939) states that "One of the natural coverts on the Kellogg Farm that appeared to be most favored by rabbits in fall and winter was a cut-over oak and hickory brush area . . . the 5-acre plot contained a large number of old skunk and woodchuck burrows that were intensively used by the rabbits." As a contrast, it has been shown in Pennsylvania that where the food and cover of the varying hare was destroyed by deer, the number of hares decreased greatly (Luttringer and Gerstell, 1939).

Effect of cover on catch of cottontails during winter.—During winter, a catch equal to 0.78 per cent of the trap night was secured in areas which in summer had a forest canopy less than 12.5 per cent dense; areas with a 25 per cent canopy yielded a 1.74 per cent catch; 50 per cent canopy, 1.10 per cent catch; 75 per cent canopy, 2.39 per cent catch; and under canopies which were denser than 87.5 per cent, the catch was equal to 3.63 per cent of the trap nights. Accordingly, the catch of rabbits during winter was highest in areas with the denser stand of trees (dense canopy during summer), a condition which is the reverse of that found during spring, summer and fall seasons (Table 8). The figures for winter catch, however, are small and probably undependable, because they are based only on trapping records from the Artificial Burrow, Brush-pile, Check, and Removal Areas. During the winter, rabbits migrated from two of the study areas even from the denser stands of large crowned trees which here appear to be most frequently occupied at this season. In two other areas (one provided with an abundance of artificial burrows, the other provided with an abundance of brush piles), the rabbits avoided the more open places and made considerable use of the artificial cover in the denser stands of trees, but only where a sufficient amount of food was available.

Summary of effect of cover on catch of cottontails. — During spring, summer and fall, cottontails preferred to occupy areas which had a minimum of large crowned trees, but in which generous amounts of shrubby vegetation occurred. In winter, however, they migrated to the lowland unless additional cover such as artificial holes and brush piles were provided. Where such cover was provided, the rabbits used it during winter most frequently among the denser stands of trees, but only where a sufficient amount of food was available.

DISCUSSION

At the rate of reproduction found during this investigation, adult female cottontails may bear as many as 22 young per season (four litters at 5.4 young per litter). Accordingly, factors other than reproductive rate are limiting cottontail populations on the areas.

Competition for home sites or territories by adult females may at times serve to limit populations, but did not do so here because there seemed to be an excess of suitable home sites available. It is recognized that rabbits which occupied the least favorable sites probably suffered greatest mortality by predation.

Intensive study of a 160-acre area revealed that only about one out of every five young survived until fall (Haugen, unpublished manuscript). It is not known that disease or parasites caused any appreciable loss on the areas studied.

Predator pressure is evidently exerted throughout the year, but no continued precise measure of it was secured. The population of predators on the areas appeared to be only average.

In general, there was a deficiency in prey species on the sandy upland areas. This deficiency, coupled with inadequacy of escape cover, makes the cottontail on these areas particularly vulnerable to predation.

Summary

A two-year intensive field study on the cottontail rabbit at the Swan Creek Wildlife Experiment Station at Allegan, Michigan, has shown the following:

The winter food of the cottontails on the upland areas consists mainly of the bark and twigs of white oak, flowering dogwood, sassafras, black oak, and New Jersey tea in the order listed.

As many as four litters in a single season are reared in this region by a single female, and the females apparently breed immediately after parturition. The average number of young per litter during the period of study was 5.4.

Weights of cottontails have varied according to sex, pregnancy, age, season, and weather. The average weight during the hunting season is 3 lbs. 3 oz. for the females, 3 lbs. 2 oz. for the males, and about 2.5 lbs. for the immature.

The most important enemies of the cottontail in the region are weasels, stray dogs, feral cats, and hawks (red-tail, broad-wing, and marsh). Experiments on the vulnerability of cottontails in an artificial burrow have shown that they are capable of escaping or defending themselves in such quarters.

An ecologic relationship between the population density of cottontails and the density of the prevailing ground cover of shrubs has been demonstrated; namely, that rabbits most frequently occupy areas with a generous amount of low ground cover, and may completely avoid locations with a dense forest canopy and no ground cover.

Appendix

CHECK-LIST OF PLANTS

The species of plants listed here are found on the sandy upland areas of the Swan Creek Wildlife Experiment Station, Heath and Valley townships, Allegan County, Michigan. Almost all species were collected on the cottontail rabbit study areas. Except where otherwise stated, the identifications were made by Betty M. Robertson of the Department of Botany, University of Michigan. Source of nomenclature is that of Deam's "Flora of Indiana" (1940).

Herbs:

Ambrosia elatior L. (Common Ragweed)

Andropogon furcatus Muhl. (Big Blue-stem)

Anemone virginiana L. (Tall Anemone)

Antennaria plantaginifolia L. (Plaintain-leaf Pussytoes)

Apocynum androsaemifolium L. (Spreading Dogbane)

Aquilegia canadensis L. (American Columbine)

Arabis lyrata L. (Lyreleaf Rockcress)

Arenaria stricta Michx. (Rock Sandwort)

Aronia arbutifolia (L.) Ell. (Chokeberry)

Artemisia caudata Michx. (Wormwood)

Asclepias amplexicaulis J. E. Smith (Milkweed)

Asclepias tuberosa L. (Butterflyweed)

Asparagus officinalis (Tourn.) L. (Garden Asparagus)

Aster azureus Lindl. (Azure Aster)

Aster Drummondii Lindl. (Drummond Aster)

Aster laevis L. (Smooth Aster)

Aureolaria virginica (L.) Farw. (Downy False Foxglove)

Brassica kaber var. *pinnatifida* (Stokes) Wheeler (Charlock)

Caltha palustris L. (Marsh Marigold)*

Campanula rotundifolia var. *intercedens* (Witasek) Farw. (Harebell)

Cardamine bulbosa (Schreb.) BSP. (Bulb Bittercress)*

Carex pennsylvanica Lam. (Sedge)

Claytonia virginica L. (Virginia Spring Beauty)

Comandra Richardsiana Fern. (Richards Bastard Toadflax)

Coreopsis lanceolata L. (Lance Coreopsis)

Coreopsis lanceolata var. *villosa* Michx.

Cyperus filiculmis Vahl.

Desmodium viridiflorum (L.) Beck (Velvet-leaf Tickclover)

Epigaea repens L. (Trailing-arbutus)

Eragrostis spectabilis (Pursh) Steud. (Purple Lovegrass)

Erigeron pulchellus Michx. (Robin's Plantain)

Erigeron ramosus (Walt.) BSP. (Narrowleaf Whitetop)

Erodium cicutarium (L.) L'Her. (Storksbill)

Euphorbia corollata L. (Flowering Spurge)

Euphorbia Cyparissias L. (Cypress Spurge)

Fagopyrum esculentum Moench. (Buckwheat)

Fragaria virginiana Duchesne (Virginia Strawberry)

Gaultheria procumbens L. (Wintergreen)

Geranium maculatum L. (Wild Geranium)

Gnaphalium obtusifolium L. (Old-field Balsam)

Helianthemum canadense (L.) Michx. (Rockrose)

Helianthus divaricatus L. (Sunflower)

Helianthus occidentalis Riddell. (Sunflower)

Hepatica americana (DC.) Ker. (Round-lobe Hepatica)

Hypericum perforatum L. (Common St. Johnswort)

Koeleria cristata (L.) Pers. (Junegrass)

Krigia virginica (L.) Willd. (Dwarf Dandelion)

Lepidium virginicum L. (Peppergrass)

Lespedeza virginica (L.) Britt (Slender Bushclover)

Liatris cylindracea Michx. (Gayfeather)

Liatris scariosa (L.) Willd. (Gayfeather)

Linaria canadensis L. Dumort. (Toadflax)

Lithospermum canescens (Michx.) Lehm. (Puccoon)

Lupinus perennis L. (Sun-dial Lupine)

Lycium halimifolium Mill. (Common Matrimony-vine)

Lysimachia lanceolata Walt.

Oenothera pycnocarpa Atkinson & Bartlett. (Evening-primrose)

Oenothera cymatilis Bartlett.

Opuntia humifusa Raf. (Prickly Pear)

Osmunda cinnamomea L. (Cinnamon Fern)

Panicum depauperatum Muhl. (Panicum)

- Panicum pseudopubescens* Nash. (Panicum)
Pedicularis canadensis L. (Early Wood-betony)
Penstemon hirsutus (L.) Willd. (Eastern Penstemon)
Poa pratensis L. (Kentucky Bluegrass)
Polygala polygama Walt.
Polygonatum canaliculatum (Muhl.) Pursh. (Solomon's Seal)
Polystichum acrostichoides (Michx.) Schott (Christmas Fern)
Potentilla recta L. (Cinquefoil)
Potentilla simplex Michx. var. *typica* Fern (Cinquefoil)
Prunella vulgaris var. *lanceolata* (Bart.) Fern. (American Shelfheal)
Pyrula elliptica Nutt. (Shinleaf)*
Ranunculus fascicularis Muhl. (Tufted Buttercup)
Ranunculus hispidus Michx. (Bristly Buttercup)*
Saponaria officinalis L. (Bouncing-bet)
Selaginella rupestris (L.) Spring. (Rock Selaginella)
Senecio aureus L. (Golden Groundsel)
Smilacina racemosa (L.) Desf. (False Solomon's-Seal)
Solidago caesia L. (Wreath Goldenrod)
Solidago canadensis L. (Canada Goldenrod)
Solidago nemoralis Ait. (Old-field Goldenrod)
Stipa avenacea L. (Blackseed Needlegrass)
Stipa spartea Trin. (Porcupine Grass)
Tephrosia virginiana (L.) Pers. (Smooth-leaflet Virginia Goatrue)
Tradescantia canaliculata Raf. (Glaucous Spiderwort)
Tragopogon pratensis L. (Goatsbeard)
Trillium grandiflorum (Michx.) Salisb. (Large flower Trillium)
Verbascum Thapsus L. (Mullein)
Verben canadensis (L.) Britt. (Rose Verbena)
Vicia Cracca L. (Vetch)
Vicia villosa Roth. (Hairy Vetch)
Viola conspersa Reichenb. (Dog Violet)*
Viola sagittata var. *ovata* (Nutt.) T. & G.
Viola pallens (Banks) Brainerd (Smooth White Violet)*
Viola pedata L. (Birdfoot Violet)
Viola sororia Willd. (Downy Blue Violet)
Vitis palmata Vahl. (Catbird Grape)
- Shrubs:
Alnus incana (L.) Moench var. *americana* Regal. (Speckled Alder)*
Amelanchier canadensis (L.) Medic. (Downy Shadblow)
Amelanchier humilis Wieg. (Low Shadblow)
Ceanothus americanus L. (New Jersey Tea)
Chamaedaphne calyculata (L.) Moench. (Leatherleaf)*
Cornus florida L. (Flowering Dogwood)
Cornus racemosa Lam. (Gray Dogwood)
Crataegus sp. (Hawthorn)
Gaylussacia baccata (Wang.) K. Koch. (Black Huckleberry)
Rhus typhina L. (Staghorn Sumac)
Ribes americanum Mill. (American Black Currant)
Rosa palustris Marsh. (Swamp Rose)
Rosa carolina L. (Pasture Rose)
Rubus allegheniensis Porter (Allegheny Blackberry)
Rubus flagellaris Willd. (Northern Dewberry)
Salix humilis Marsh. (Prairie Willow)
Salix sp. (Willow)*
Vaccinium corymbosum L. (Highbush Blueberry)*
Vaccinium angustifolium Ait. (Lowbush Blueberry)
Vaccinium vacillans Kalm ex Torrey. (Dryland Blueberry)
Viburnum acerifolium L. (Mapleleaf Viburnum)
- Trees:
Acer rubrum L. (Red Maple)
Carya ovalis (Wang.) Sarg. (Small-fruited Hickory).
Malus coronaria (L.) Mill. (Wild Sweet Crab)
Malus pumila L. (Common Apple)
Ostrya virginiana (Mill.) K. Koch. (Hop-hornbeam)
Pinus resinosa Ait. (Norway Pine)
Pinus Strobus L. (Northern White Pine)
Populus alba L. (White Poplar)
Prunus serotina Ehrh. (Black Cherry)
Prunus virginiana L. (Common Choke-cherry)
Quercus alba L. (White Oak)**
Quercus velutina Lam. (Black Oak)
Sassafras albidum (Nutt.) Nees. (Sassafras)

* Taken at the edge of a leather leaf bog.

** Identification by the writer.

REFERENCES

- ALIEN, D. L. 1938a—Ecological studies on the vertebrate fauna of a 500-acre farm in Kalamazoo County, Michigan. *Ecol. Mon.* **8**:347-436.
- 1938b—Breeding of the cottontail rabbit in southern Michigan. *Am. Midland Naturalist* **20**:464-469.
- 1939—Michigan cottontails in winter. *Jour. Wildlife Management* **3**:307-322.
- BEULE, JOHN D. 1940—Cottontail nesting study in Pennsylvania. *Pennsylvania Game News* **11**(2):10-11, 28.
- DICE, LEE R. 1929—An attempt to breed cottontail rabbits in captivity. *Jour. Mammalogy* **10**:225-229.
- 1933—A correction concerning the species of cottontail that bred in captivity. *Ibid.* **14**:162.
- FIPPIN, ELMER O. AND THOMAS RICE. 1901—Soil survey of Allegan County, Michigan. U. S. Department of Agriculture, Bureau of Soils Third Rept. 93-124.
- GERSTELL, RICHARD 1937a—Management of the cottontail rabbit in Pennsylvania. *Pennsylvania Game News* **7**(12):6-7, 27, 30.
- 1937b—Management of the cottontail in Pennsylvania. *Ibid.* **8**(2):8-11, 32.
- HAMILTON, W. J., JR. 1939—American mammals, their lives, habits, and economic relations. McGraw-Hill, New York and London.
- HAMMOND, JOHN, AND F. H. A. MARSHALL. 1925—Reproduction in the rabbit. Edinburgh: Oliver and Boyd. 210 pp.
- HAMMOND, JOHN 1931—The process of reproduction in the rabbit. *Zeitschrift für Pelztier-und Rauchwarenkunde*, Band **3**, Verlag der Reichs-zentrale für Pelztier und Rauchwaren-Forschung, Leipzig.
- HAUGEN, ARNOLD O. 1942—Home range of the cottontail rabbit. *Ecology*, in press.
- Unpublished manuscript. Management studies of the cottontail rabbit in southwestern Michigan. **97 pp.**
- HICKIE, PAUL. 1940—Cottontails in Michigan. Game Division, Michigan Department of Conservation.
- INGERSOLL, ERNEST. 1907—The life of animals. The Macmillan Company, sec. ed.
- INGLES, LLOYD G. 1941—Natural history observations on the Audubon cottontail. *Jour. Mammalogy* **22**:227-250.
- KENNICOTT, ROBERT. 1857—The quadrupeds of Illinois injurious and beneficial to the farmer. Ex. Doc. 32, 35th. Congress, 1st Session: Rept. Commissioner Patents 1857, Agriculture, Washington 1858. 72-107.
- LEVERETT, FRANK 1917—Surface geology and agricultural conditions of Michigan. Michigan Geological and Biological Survey Pub. 25, Geological Series **21**: Wynkoop Hallenbeck Crawford Co., Lansing, Michigan.
- LUTTRINGER, LEO A. AND RICHARD GERSTELL. 1938—Pennsylvania Wildlife. Pennsylvania Game Commission, Harrisburg, Bull. **18**:1-48.
- MORTON, JAMES N. AND JOHN B. SEDAM. 1938—Cutting operations to improve wildlife environment on forest areas. *Jour. Wildlife Management* **2**(4):206-214.
- MCATEE, W. L. 1930—Propagation of upland game birds. U. S. Department of Agriculture Farmers' Bulletin No. 1613.
- SETON, E. T. 1929—Lives of game animals. Doubleday, Doran and Co., Garden City, New York, 4 vol.
- TRIPPENSEE, R. R. 1934—The biology and management of the cottontail rabbit. Univ. Michigan School Forestry and Cons. Unpublished Thesis.
- 1936—The reproductive function in the cottontail rabbit (*Sylvilagus floridanus mearnsii* Allen) in southern Michigan. North Am. Wild. Conf. Proc., 344-350.
- VEATCH, J. O. 1933—Agricultural land classification and land types of Michigan. Michigan State Coll. Agricultural Exp. Sta. Special Bull. **231**:1-51.
- VORHIES, CHARLES T. AND WALTER P. TAYLOR. 1933—The life histories and ecology of jack rabbits, *Lepus alleni* and *Lepus californicus* sp., in relation to grazing. Univ. of Arizona Tech. Bull. **49**:471-587.

